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Boreal Hepaticae, a Manual of the Liverworts of Minnesota and Adjacent Regions

II. Ecology (continued)

Rudolf M. Schuster
University of Michigan, Ann Arbor

Hepatic Communities and Their Relationships to the Vascular Flora

We have seen earlier that the microclimatically and microedaphically controlled unistratal bryophyte-lichen communities are to a degree independent of the macroenvironment formed both by climate and tree-cover. However, this is true only within certain limits, and it would be more correct to state that these communities are independent of the macroenvironment *only when* the macroenvironment as a whole includes microenvironments suitable for the development of these communities.

Therefore, we find major climatic conditions decidedly influencing the distribution of many species (see p. 203), even if not in exactly the same fashion as the macroclimate conditions the occurrence of the dominant vascular vegetation. This warrants treatment of the hepatic communities in four groups, which are largely correlated with the vascular vegetation, as follows: 1) Arctic-alpine communities (limited largely to the tundra strip along the Lake Superior shore); 2) Boreal communities (limited largely to the coniferous forests); 3) Communities of southern affinity, essentially not occurring north of the deciduous forests (limited to the deciduous forest region); 4) Xerothermophyte communities, with a well-developed adaptation to dry and hot conditions (limited to the prairie regions).*

For that reason, the hepatic communities will be dealt with in connection with the basic plant formations of which they are a part. It is, in general, only *within* each of these major vegetational formations that we find the bryophyte-lichen communities showing any degree of independence of the

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* It must, of course, be kept in mind that "islands" of vegetation very often exist within otherwise homogeneous vegetation, differing much in nature. Examples are the coniferous and ericad bog vegetations in pockets of the deciduous region (the Hepaticae of which all belong to coniferous region types), and the pockets of prairie vegetation on exposed knolls or on sunny bluffs, in the deciduous forest region. For that reason, it must not be expected that species of Hepaticae normally restricted to areas mapped as coniferous forest (fig. 23) cannot occur as occasionals in the deciduous region. In the section on *Phytogeography*, the historical reasons why such boreal types may persist in isolated stations south of their normal distribution are dealt with. In other words, not only do the existing macroenvironment and microenvironment condition the occurrence of a species, but its occurrence is also influenced by historical factors.

Figs. 21-22.—21. The "Tundra Strip," in the foreground a rock-pool area with the *Scapania degenii-irrigua-Odontoschisma macounii* Associule well-developed (see p. 262). On the left hand side of the island, in the distance, the cliff communities (pp. 265-274) well developed. Long Island, Susie Islands, Lake Superior. 22. Acid bog succession. In the foreground open Sphagnum-sedge mat; fringed by *Chamaedaphne*, in the background black spruce, tamarack and white pines.
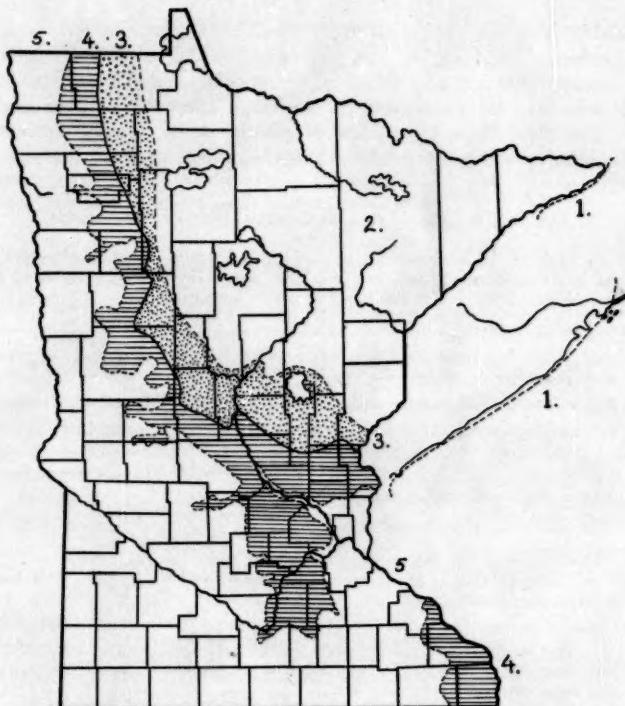
Fig. 23.—Vegetational regions of Minnesota. 1. The "Tundra Strip;" 2. Coniferous Forest; 3. Ecotone between Coniferous Forest and Deciduous Forest; 4. Deciduous Forest; 5. Prairie. The inset showing more accurately the restriction of the Tundra Strip, from The Point, at Grand Marais, to Pigeon Point and the Susie Islands.

variations in vegetation types. The associated map (fig. 23), showing the distribution of the major formations in Minnesota, clearly indicates the restriction of the associated cryptogamic societies.*

* This map is based largely upon that in Rosendahl and Butters, *Trees of Minnesota*, with the following change: I have indicated a narrow microclimatically and microedaphically controlled "Tundra Strip" adjacent to Lake Superior, from The Point, Grand Marais, northeastward.

This map disagrees with the concepts of E. L. Braun (*The deciduous forests of eastern North America*), who would consider all of the northeastern one-third of the state as belonging to the beech-maple-hemlock-yellow birch-white pine forest type. Such a disposition of the region seems difficult to accept, for the following reasons: 1) Beech is absent; 2) Sugar Maple is very rare and occurs only as a relict of the xerothermic period; 3) Hemlock is totally absent; 4) The dominant trees, in undisturbed forest throughout this area, are spruce, fir, with admixed *Sorbus* and *Betula papyrifera* (and its var. *cordifolia*), with the subclimax trees being white pine (rarely postclimax), red pine, and the scrubby *Pinus banksiana* in dry areas, while black spruce and tamarack are the common hydrarch subclimax trees.

Within both the coniferous forest (and local tundra strip) region and the deciduous forest region, the following essential outline of the crypto-gamic communities is used. Many of the associules listed for the coniferous-tundra area have no counterpart (or are much attenuated) in the deciduous area. The third large region, the prairie, is almost lacking in bryophyte communities, so will be very briefly treated.

KEY TO THE CHIEF TYPES OF COMMUNITIES OF THE REGION

On the basis of the habitat, we may distinguish a group of community-types, which are found in the coniferous as well as (to a lesser extent) in the deciduous forest regions; a very few of these communities also occur in prairie habitats.*

A. Plants growing attached .... B

  B. Plants undergoing ecesis on a firm substrate (rock, tree-trunks, etc.), *or* invading
    such sites after deposition of a relatively thin humus or peat layer C

    C. Plants over bark of trees or on logs: epiphytic or epixylic .... D

      D. Occurring over bark of living trees—epiphloemic (or corticolous) communities
                      In coniferous forest ....p. 275
                      In deciduous forest ....p. 293

      D. Occurring over decaying wood—epixylic communities
                      In coniferous forest ....p. 276
                      In deciduous forest ....p. 294

    C. Plants occurring over rocks, or associated with rocks (in rock-crevices, or on thin
      soil, or peat-layers over rocks; or over rocks in water). Epipetric and chasmo-
      phytic communities
                      In coniferous forest ....pp. 262, 274
                      In deciduous forest ....p. 289

  B. Plants undergoing ecesis over a loose substrate (sand, humus, peat), *not* merely a
    thin layer over rock outcrops .... E

    E. On largely organic substrates .... F

      F. Non-helophytic, occurring on humus or much-decayed logs ....G

        G. Occurring on decaying logs (see D, above)

        G. Occurring on humus—humicolous communities ....pp. 278, 295

      F. Helophytic: occurring in swamps and bogs on saturated soils—helophytic
        communities.
                      In coniferous forest ....p. 279
                      In deciduous forest ....p. 295

    E. On totally or largely inorganic substrates .... H

      H. Plants without a long resting period; perennials I

        I. Over sandy, loose soils—arenicolous communities
                      In coniferous forest ....p. 286
                      In deciduous forest ....p. 296

        I. Over compact, clayey or loamy soils, usually on banks
                      In coniferous forest ....p. 287
                      In deciduous forest ....p. 296

      H. With a long resting period; usually in open, sunny areas .... J

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    * It is possible to run down a particular species, via the present key, to the proper community-group, leading direct to the detailed treatment on the following pages. The present outline is based partly on that of Gams (*in* Verdoorn, 1932).

CONIFEROUS FOREST FORMATION (AND THE TUNDRA STRIP)

In the northeastern one-third of Minnesota the predominant forest trees consist of evergreens, with the deciduous trees (other than paper birch) forming a minor element, except in the subclimax. This association of coniferous trees includes such species as fir (*Abies balsamea*), spruce (*Picea glauca* and *nigra*) and more exclusively in swampy and boggy areas, tamarack (*Larix occidentalis*) and white cedar (*Thuja occidentalis*). The latter two species are frequent in the hydrarch subclimax. On drier ground, especially on dry ridges and on sand plains, various pines (*Pinus banksiana* and *P. resinosa*, chiefly) occur. Since Hepaticae are rarely found in this xerarch subclimax, it will not be further discussed here. Associated with these coniferous trees are several deciduous trees, chiefly mountain ash (*Sorbus*) and white or paper birch (*Betula alba* and its variety *cordifolia*).

At the edge of Lake Superior, there is, in addition, a variably wide zone with no arborescent vegetation, because of the cold waters of Lake Superior, ice and wave action, and the inability of a soil-layer to accumulate over the rocks adjacent to the shoreline. This zone may be considered to represent a narrow, edaphically and microclimatically controlled treeless or tundra zone, which in many ways approximates the tundra or treeless regions of the arctic and of alpine summits. The most characteristic plants of this tundra strip and various Vacciniaceae (*Vaccinium uliginosum, V. vitis-idaea, V. oxycoccus, Andromeda glaucophylla, Ledum*), *Polygonum viviparum, Selaginella selaginoides, Primula mistassinica, P. intercedens, Pinguicula vulgaris, Sagina nodosa, Scirpus cespitosus, Trisetum spicatum, Empetrum atropurpureum, Deschampsia flexuosa, Tofielda pusilla, Geocaulon lividum, Euphrasia hudsonica, Potentilla tridentata, Potentilla fruticosa*. This zone along the shoreline and adjacent to the forested region thus supports two distinct communities that recur again far to our north: a hydrarch *Scirpus cespitosus-Primula-Pinguicula* society around sunny rock-pools, and an acid, xerarch *Empetrum-Vaccinium* heath over moist ledges.

The layer societies (associules) that occur in these two general regions and in which Hepaticae play an important part, may be briefly treated as follows. In this discussion an effort is made to characterize these societies also by the vascular plants that frequently undergo ecesis or occur with the

bryophyte layer societies; although desirable, limits of space quite preclude giving a detailed account of associated mosses.

EPIPETRIC COMMUNITIES

We will consider here the truly epipetric communities, which are essentially pioneers on bare rocks, *as well as* those communities, such as the *Mylia-Odontoschisma* facies of the *Mylia-Cladopodiella* associule, which do not occur on bare rock, but represent end-points in succession from communities that start on bare rock. It is totally impossible to draw an arbitrary line between such strictly epipetric types and the communities which undergo ecesis only after a variably thick peat or soil-layer has accumulated. Therefore, all communities associated with rock-outcrops, whether they occur over rocks, on soil in rock-crevices, or over peaty soil or peat over rock-ledges, will be treated here. In that way, some of the more obvious successional principles can be elucidated, and communities that stand in obvious successional relationship to each other can be treated together.

TERRESTRIAL COMMUNITIES

The terrestrial communities, including those associules which are exposed to air, except under very unusual (and intermittent, unpredictable) conditions, will be treated under three categories: firstly, a group of pioneer communities of "heliophile" species, occurring usually in full sun, growing around rock-pools; secondly, a group of pioneer (or near-pioneer) species of relatively shaded rocks, varying from very dry to wet (but if wet, then moistened by running water); thirdly, we will deal with the bryochameaphytic, humicolous associules which are to be derived directly, by succession, from the first two categories of pioneer communities. Though the pioneer communities start out under very different physical conditions, we find, as is to be expected, that as ecological conditions advance, we have succession towards a more uniform type of community, which will be dealt with as an appendix to the third group.

PIONEER ROCK-POOL COMMUNITIES

Societies occurring at the edges of rock-pools, or in rock-crevices or over rock-faces where there is much seepage, in sunny, exposed sites (usually within 3-25 ft. of Lake Superior). The societies are much more widely distributed in the tundra, and locally are limited largely to the "tundra strip" and include a large number of northern species. Two very different associules can be distinguished around rock-pools and moist sunny crevices, depending on the nature of the underlying rocks.

1. *"Basiphile" Scapania degenii-irrigua-Odontoschisma macounii Associule.* —Around rock-pools and "run-off" crevices of basic rocks (basalts, diorite, shales and sandstones) near the Lake Shore we find a sharply defined community characterized by the following vascular plants: *Primula mistassinica, Polygonum viviparum, Selaginella selaginoides, Potentilla fruticosa, Pinguicula vulgaris,* occasionally *Euphrasia hudsonica* and *Hudsonia ciliolata, Aster ptarmicoides,* but especially *Scirpus cespitosus.* Under the xeric extremes

under which we find this associule, *Potentilla tridentata* also occurs, and under moist extremes, we occasionally find *Drosera rotundifolia.* Typically, most of the Hepaticae occur around the bases of *Scirpus* hummocks. Several different phases occur, as regards the associated Hepaticae. The measured pH varies from 5.5-7.0.

A. SCAPANIA DEGENII-ODONTOSCHISMA MACOUNII FACIES: The characteristic Hepaticae, in addition to the above type members, are secondary species such as *Scapania irrigua,* *Lophozia (Leiocolea) gillmani,* more rarely *schultzii* and *heterocolpa,* *Tritomaria quinquedentata,* *Ptilidium ciliare* and *Cephaloziella hampeana.* This community is developed best on several of the Susie Islands (Sailboat I., Long I., Big Susie I.) and at Grand Marais (here it forms the matrix for *Selaginella* and *Tofieldia glutinosa!*); traces of it also occur south of the mouth of the Temperance River.

B. SCAPANIA IRRIGUA-RICCARDIA PINGUIS FACIES: In addition to these two species, *Cephaloziella hampeana* is a characteristic associated species. This associule occurs south of the mouth of the Temperance River, and at Gooseberry River; sometimes the *Riccardia pinguis* is lacking. At the Temperance R., the *Scirpus* hummocks to which this associule is confined, support not only *Primula,* *Pinguicula* and *Aster ptarmicoides,* but also *Drosera rotundifolia.*

2. "Calciphobe" *Gymnocolea-Cephalozia bicuspidata Associule.*—Around rock-pools and in moist crevices of sunny rocks, of non-basic rocks, a pioneer associule, formed largely by *Gymnocolea inflata* and *Cephalozia bicuspidata,* undergoes ecesis. Several different faciations of this occur. The associated vascular species are largely members of the *Empetrum-Vaccinium* heath, such as *Ledum, Chamaedaphne, Vaccinium vitis-idaea, Potentilla tridentata,* etc. Depending on the locus of occurrence, and to some degree on succession, two major facies can be distinguished, the first of which has been previously noted by the author (Schuster, 1949) for central and western New York.

A. GYMNOCOLEA INFLATA-CEPHALOZIA BICUSPIDATA FACIES: Occurring as pioneers over moist acidic rocks, especially along run-off crevices of ledges and rocks, where insolation is usually high. In addition to the two type members, we occasionally find *Scapania nemorosa* and *irrigua* undergoing ecesis here. This facies occurs again over moist crests of cliffs, where there are seepage and much insolation (as at Gunflint Lake), and then is often associated with *Cephaloziella byssacea.* Around acid rock-pools the community often occurs with *Lophozia kunzeana,* and then grades into the next facies. The measured pH (Big Susie I.) varied from 3.8 to 4.8. At the juncture with peaty, sphagnous hummocks, this pioneer community often "grades" into the *Mylia-Odontoschisma-Calypogeia* facies that invades the surface of peat; there it occurs with *Mylia anomala, Cephalozia media, Bazzania trilobata,* under a pH between 4.1-4.3. This community is extremely well developed on the rocky shores of the Susie Islands, but scarcely occurs elsewhere in Minnesota.

B. GYMNOCOLEA INFLATA-LOPHOZIA KUNZEANA FACIES: Occurring, usually as a more secondary society, over thicker, spongier, peatier soil, often directly over *Sphagnum,* usually in thick mats at the edges of sunny rock-pools (as on Belle Rose I. and at Grand Marais). Associated usually are a well-developed heath (characteristically *Ledum, Vaccinium* sp.), *Drosera rotundifolia,* and *Sphagnum.* Other associated Hepaticae are *Ptilidium ciliare, Lophozia ventricosa,* occasionally bog forms of *Lophozia barbata,* occasionally *Cephaloziella rubella* or *hampeana.* (At Grand Marais the society is typically developed, except that *Gymnocolea* is absent.)

This community has been studied most extensively on Porcupine Island, where twelve plots, each 6 x 12 in., lying in a transect, were studied. The data derived from these are summarized in table 3. It should be noted that

the communities were all exposed to full sun, except for very partial shade (derived from an *Alnus* shrub, some plants of *Ledum groenlandicum*, and small forbs such as *Potentilla tridentata*, *Vaccinium vitis-idaea*, *Carex* sp., *Drosera rotundifolia*); a few plants of *Chamaedaphne calyculata* also forming some shade. pH (one measurement), 4.1, but probably varying from *ca.* 3.7-4.5 or more.

TABLE 3.—Transect of pool, N. end of Porcupine I., Susie Islands, Minnesota. Stations 1 and 12 on bare rock, in sunny, run-off crevices, with plants of *Vaccinium uliginosum* and *Potentilla tridentata* present; station 2, pure *Sphagnum* polster; station 3, wet, periodically inundated rock surface, in full sun, no vascular plants present; between this and station 4 a permanent, *Drepanocladus*-filled pool; station 4, edge of *Drepanocladus* pool (the mat of *Gymnocolea* up to 1.5 in. thick, with pure peat below, formed by pure *Drepanocladus*, indicating succession from hydric *Drepanocladus* to hygric *Gymnocolea* stage); stations 5-7 intermittently dry rocks, above normal water-level, in partial shade of *Chamaedaphne*; station 8, peaty, constantly moist edge of *Sphagnum* polster; stations 9-10, peaty polster, covered by *Gymnocolea-Lophozia kunzeana* stage, over older *Sphagnum* community; station 11, juncture of dry rock-surface and peaty polster; station 12, similar to station 1.

The cover (in percent) given is based on two estimates (higher and lower figures). In some cases, in this and succeeding tables, total cover may total more than 100%, owing to the fact that the minute species (*e.g.*, *Cephaloziella rubella*) may creep over other, more robust species (such as *Lophozia kunzeana*).

Species			Plot			
	1	2	3	4	5	6
Gymnocolea inflata	90-95%	......	85-90%	90-94%	1-3%	8-10%
Mosses	5-9	......	5	......	1-2	......
Ptilidium ciliare	<0.1	......	......	......	......	......
Sphagnum	......	100	3-5	......	......	<5
Lophozia ventricosa	......	......	<2	......	10-12	......
Polytrichum	......	......	tr	......	1	......
Cephaloziella rubella	......	......	......	<0.1	70-85	60-70
Lophozia kunzeana	......	......	......	4.5	<0.1	......
Dicranum	......	......	......	......	......	3-4
Scapania mucronata	......	......	......	......	......	12-18
Drepanocladus	......	......	......	<1	......	......
Scapania irrigua	......	......	......	......	......	......

TABLE 3 (*Continued*)

Species	Plot					
	7	8	9	10	11	12
Gymnocolea inflata	tr	80-85%	80-85%	45-50%	......	99
Mosses	......	2	3-5	4-5	6-8	<0.5
Ptilidium ciliare	......	......	......	......	......	tr
Sphagnum	......	......	1-3	3-5	2-3	......
Lophozia ventricosa	......	3	<1	......	......	......
Polytrichum	......	......	<0.5	......	......	......
Cephaloziella rubella	75-80	2-5	......	......	3-5	......
Lophozia kunzeana	......	10-12	......	30-35	75-80	......
Dicranum	......	<5	2-3	5-8	......	......
Scapania mucronata	......	......	......	......	......	......
Drepanocladus	15-20	......	5-8	......	2-3	......
Scapania irrigua	......	......	2-3	......	......	......

PIONEER CLIFF COMMUNITIES

Communities occurring as pioneers or near-pioneers on shaded, moist ledges and cliff-walls (either along the shore of Lake Superior, or in the ravines that lead into it; elsewhere these societies are present in a much diluted form, as at Lake of the Woods, and in the lake region of northeastern Minnesota adjacent to Canada). Unlike the preceding two associules, the present communities are not sharply restricted to the lake shore, i.e., they occur both in the "Tundra Strip," and over cliffs and ledges in the coniferous zone proper. These communities have been studied in detail both on the basaltic rocks of Lake Superior (and the adjacent ravines; in the Clearwater Lake and Gunflint Lake region; in Lake of the Woods), as well as in Wisconsin (chiefly Apostle Islands) and in the Keweenaw Peninsula of Michigan and at Marquette and Munising in Michigan. The communities represented here are extremely diverse and rich in species, and very difficult to satisfactorily separate into groups. The most obvious separation between these communities is on the basis of their calcium tolerance (whether "calciphile" or "calciphobe") and on the basis of whether they are pioneer species or secondary invaders, and whether the species are xerophytic, mesophytic, or hygrophytic. Concurrent with the great variability of the communities, the associated

vascular flora also varies very greatly, and will be briefly treated under each separate associule.

For the sake of simplicity, the communities are arbitrarily treated without attempting to indicate successions that occur in some cases.

1. Pioneer societies—over bare rock only; societies with little or no further succession 2
   2. Xerophyte communities originating on bare, often sunny rock-walls 3
      3. Over exposed vertical rock-walls in areas of direct light ....
      ....*Frullania-Radula-Porella* associule
      3. Over dry talus boulders or crests of ledges ....*Ptilidium-Cladonia* associule
   2. Meso-hygrophyte communities, usually undergoing ecesis in areas with diffuse light
      only ....*Lophozia-Scapania* associule, *Marsupella-Scapania* facies
1. Open societies, able to undergo some succession; usually not strictly pioneer in nature
   (all variations of the *Lophozia-Scapania* associule) 4
   4. Calciphile 5
      5. Mesophytic; usually in spray or wave-action zone ....
      ....*Leiocolea-Preissia-Scapania* facies
      5. Xerophytic; usually on relatively sunny rocks ....
      ....*Lophozia barbata-Lophocolea minor-Tritomaria quinquedentata* facies
   4. Calciphobe 6
      6. Mesophytic ....*Lophozia alpestris-Scapania nemorosa* facies
      6. Xerophytic ....*Lophozia alpestris-Andreaea* facies

These seven communities belong to three major types, 1) the widespread *Frullania-Radula-Porella* associule (an associule showing little succession), 2) the xeric *Ptilidium-Cladonia* associule, and 3) the more ubiquitous and variable *Lophozia-Scapania* community. In the tundra and coniferous regions, the *Lophozia-Scapania* associule is the predominant one on all of the rocks and ledges, except those so dry that they are limited to the *Frullania-Porella-Radula* or *Ptilidium-Cladonia* associules. With the tremendous expected variation in exposure, nature of the underlying rocks, moisture, slope, etc., we can expect a bewildering degree of variation in this *Lophozia-Scapania* community complex—one of the most variable and difficult of the holarctic, epipetric and chasmophytic community-groups. The following analysis is perhaps adequate for the restricted region; it will prove only partially adequate in montane areas (such as in the White Mountains of New Hampshire).

    1. *Pioneer Xerophyte Frullania-Radula-Porella Associule.*—This community is essentially identical in nature to that existing on the exposed bark of trees; in both cases, exposure is great, moisture very intermittent, the substrate usually quite dry, and competition is largely with lichens (*Umbilicaria*, etc.) and a few mosses (such as *Hedwigia, Ulota*, etc.), rather than with other Hepaticae. The associule is also a relatively stable one, with only a slight amount of succession. Typically, *Frullania asagrayana* and *Radula complanata*, more rarely *F. bolanderi, saxicola* and *eboracensis* occur; under somewhat less extreme xeric conditions *Porella platyphylloidea* and sometimes *Porella platyphylla* occur. At least four faciations can readily be distinguished.

    A. EXTREME XERIC FRULLANIA-LICHEN FACIES: Consisting, normally, merely of *Frullania asagrayana* (more rarely with *bolanderi* or *saxicola*) and lichens; occasionally with a little *Radula complanata*. Measured pH, 4.2.

B. XERIC FRULLANIA-RADULA FACIES: *Frullania asagrayana, bolanderi* and *Radula complanata* are consociated with lichens; commonly associated ferns of this rock-face community are *Woodsia silvensis , W. oregana, W. alpina, Dryopteris fragrans;* occasionally *Cystopteris fragilis* nearer the next extreme.

C. MESIC-XERIC RADULA-LEJEUNEA FACIES: Over shaded, relatively humid and sheltered cliffs (as at Gunflint Lake) occur *Radula complanata,* sometimes *R. obconica, Lejeunea cavifolia* and *Cololejeunea biddlecomiae;* the more xeric *Frullania* species are absent.

D. MESIC-XERIC PORELLA PLATYPHYLLOIDEA-RADULA FACIES: Over somewhat more exposed rocks than in C, often on horizontal or sloping ledges, often over a thin soil layer (i.e., not strictly pioneer) occur *Porella platyphylloidea* or *platyphylla,* rarely together with *Radula complanata.* These often form a closed society because of the larger and robust size of the *Porella.*

2. *Ptilidium ciliare-Cladonia Associule.*—Occurring usually over relatively dry cliffs or large talus-blocks (as at Clearwater and Mountain Lakes, on exposed talus slopes); a nearly closed community of xeromorphic mosses, with the initial species *Cladonia rangiferina* and related species, and *Ptilidium ciliare;* until the talus blocks are covered by soil, no further succession appears probable. This is a frequent community on dry talus slopes at Clearwater Lake.

3. *Various manifestations of the Scapania-Lophozia communities or associules.*—In the deciduous region, this group of communities exists in such attenuated form that treatment as a single *Scapania-Lophozia* associule (with several facies), as in Schuster, 1949, is warranted. When the various manifestations existing in the boreal and arctic-alpine regions are included, it becomes difficult to treat these highly interdigitated communities as a single associule. The following are perhaps the most distinct of the facies that can be distinguished locally.*

A. MARSUPELLA-SCAPANIA FACIES: Occurring, either in the wave-action zone (as on Oley I.) or near water falls or at the rocky edges of swift streams. This community is very abundantly developed and complex in montane areas; in the lowlands it occurs in a very attenuated form. On rocks near the wave-action zone *Marsupella emarginata* undergoes ecesis (as on Oley I., and at Grand Marais); this occurs here either by itself, or associated with *Scapania undulata* and *S. subalpina.* On such moist shaded rocks *Ptilidium pulcherrimum* is an occasional complementary species.

B. LOPHOZIA ALPESTRIS-ANDREAEA FACIES: A pioneer and near-pioneer community, getting its start on more or less shaded, sheltered, but rather dry vertical cliffs. Associated with *Lophozia alpestris* are such species as *Diplophyllum taxifolium macrosticta, Lophozia barbata, Anastrophyllum minutum, A. michauxii, Tritomaria quinquedentata,* and *Lophozia longidens.* Depending on the amount of shelter and moisture, variation occurs into the next.

C. LOPHOZIA ALPESTRIS-SCAPANIA NEMOROSA FACIES: Closely similar to B above, but developing under somewhat more shaded (or moister) conditions, under moderately to distinctly acid conditions (pH 4.2-5.5). Several variations occur.

1. *Diplophyllum taxifolium-Anastrophyllum minutum Community.*—Occurring particularly on very shaded, moist rock-walls at some distance from Lake Superior, on the

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* In montane areas, and ranging northward into the Arctic, this is one of the most characteristic and difficult of the community complexes in which Hepaticae play a large part. Very frequently mosses play a dominant role in such communities; these communities are not treated here.

interior of the Susie Islands (and at Hat Point); able to tolerate extremely low light intensities (1/50 - 1/75 direct sunlight or less), therefore sometimes found at the entrance to small caves, or on rock-faces in crevices between boulders. Under even moister conditions (and usually under somewhat greater light intensity) we find *Lepidozia reptans* and *Blepharostoma trichophyllum* undergoing ecesis, often resulting in the two communities which follow.

2. *Diplophyllum-Lepidozia-Blepharostoma Community.*—This community occurs particularly in shaded cuts through rocks, where the saturation deficit is always very low, and where only indirect light occurs (often the insolation is very low because of the dense coniferous forests); particularly well-developed on the western side of Big Susie Island.

3. *Lophozia alpestris-Scapania nemorosa Community.*—Occurring under more exposed conditions, often where there is some spray action, on rock-walls very near the lake (Big Susie I., Porcupine I., Belle Rose I.), or on rock-walls in the interior, where there is some seepage (Gunflint Lake), then sometimes with *Lophozia hatcheri* associated. In situations where there are deep shade and high humidity, but no seepage, *Lophozia silvicola* (less often *L. ventricosa* or *L. longidens*) may replace the *L. alpestris*. *Lophozia attenuata* is occasionally associated (as may be *Anastrophyllum (Sphenolobus) minutus*), accompanied at times by *Lepidozia* and/or *Blepharostoma*, at which point intergradation to the preceding two communities occurs.

D. MESOPHYTE "CALCIPHILE" LEIOCOLEA-PREISSIA-SCAPANIA FACIES: This community occurs essentially as an epipetric and chasmophytic pioneer community on moist ledges and cliff-walls.* The most characteristic species are *Lophozia (Leiocolea) gillmani*, *Scapania cuspiduligera, Scapania mucronata, Scapania gymnostomophila, Preissia quadrata*. Occasionally consociated and frequent accessory species are *Plagiochila asplenioides, Blepharostoma trichophyllum, Lophozia badensis, Tritomaria scitula* (more rarely *quinquedentata*) rarely *Scapania curta* and *Riccardia pinguis*. *Lophozia heterocolpa* comes in with advanced manifestations of this community. This associule occurs in an attenuated form in the southeastern "corner" of the state, over basic sandstones; there restricted largely to a *Preissia-Lophozia badensis-Scapania mucronata* facies. Commonly associated mosses are *Gymnostonum aeruginosum* and various other "calciphile" mosses. The measured pH which characterizes this community varies from about 6.0-7.2 or higher.

As the bryophyte mat develops the substrate becomes more acid, and then one can see very evident succession to the secondary *Lophozia heterocolpa-Tritomaria scitula-Odontoschisma macounii* associule (see p. 270).

E. XEROPHYTE "CALCIPHILE" AND "TOLERANT" LOPHOZIA BARBATA-LOPHOCOLEA MINOR-TRITOMARIA QUINQUEDENTATA FACIES: Over rocks and ledges that are more exposed, often more sunny (or higher above the ravine-floor or lake-level, where the plants are not kept wet by spray), and where moisture conditions are more intermittent, a more xerophytic community occurs. This is characterized by the very frequent presence of *Lophocolea minor, Lophozia (Barbilophozia) barbata, Tritomaria quinquedentata*, occasionally *Ptilidium ciliare, Scapania mucronata;* intermingled may occur *Radula complanata* (indicating either succession from the pioneer calciphile *Radula-Frullania-Porella* Associule, or zonational intergradation with it). Such "calciphile" ferns as *Dryopteris fragrans* and various *Woodsia* species, *ilvensis*, etc.) are frequent accompanying vascular species. Occasionally we find *Lophozia excisa*, more rarely (at Copper Harbor) *Lophozia (Orthocaulis)*

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* This community occurs almost invariably around waterfalls (as at the Caribou, Temperance, and Gooseberry rivers) or very near the Lake Superior shore (as at Copper Harbor, Michigan, on Isle Royale, at Grand Marais, on the Susie Islands), where spray from wave-action and the high humidity induced by the adjacent lake waters are significant. The common denominator for this community appears to be a very low saturation deficit at all times, a basic substrate, and relatively little direct sunlight. It occurs abundantly on the more basic ledges on the Susie Islands, as well as in most of the "ravines" of the North Shore of Lake Superior; I have also studied various modifications of it on the moist, subbasic sandstones on Sand I., Apostle Isls., Wisconsin, and on the Keweenaw Peninsula, and at Marquette, Michigan, as well as at Tobermory, Ontario (where it is only poorly developed).

quadrilobus, and *Lophozia* (*Barbilophozia*) *hatcheri* as accompanying species, together with *Cephaloziella hampeana.**

The previous communities discussed (rock-pool and cliff) have all been composed of pioneer species or species of near-pioneer status. Many of them persist, to a slight degree as a peat or humus-layer is formed; in most cases, however, there is very evident succession to more bryochamaephytic communities, that occur over a layer of organic humus. Thus the pioneer communities discussed above, by their reaction on the environment, change it sufficiently (especially as regards pH) to cause evolution towards secondary communities of less epipetric nature.

SECONDARY COMMUNITIES

Communities occurring subsequent to ecesis of the previous ones, with consequent reaction resulting in formation of a humus or peat layer. The several associations of species in this group all undergo ecesis after a layer of peat some $1/2$ in. thick or more has been deposited by the death and decay of the older portions of the plants of the previous series. In addition, there is the accumulation of loosened soil-particles, and the retention of soil particles that may have been washed in.

Correlated with the development of a humus layer there is normally a lowering of the pH, especially in the case of succession involving the "calciphilous" associules, and often (but not necessarily) evolution towards less mesic-hygric conditions.

The evolution of the following communities depends on several factors. Ledges or cliffs must possess a slight enough slope so that the weight of the accumulating humus layer and superficial moss mat will not periodically tear loose. Irregularities of the rock-surface enable small vascular species to gain a foothold and form centers about which the humus and moss mat can anchor itself. Finally, the community has to be far enough above the ravine-floor or the lake-level so that ice-action and wave-action (and accumulation of freezing spray) do not result in periodic destruction of the community. Given a satisfactory combination of the above conditions, we can generally expect succession towards various manifestations of the following communities.

I. Invading on thin humus over basic rocks; the pH over 5.5   Two communities may be mentioned in this regard, representing advanced stages from the pioneer "calciphile" societies treated previously.

1. *Xerophyte Lophozia barbata-Lophocolea minor Associule.*—This community may at times evolve from the *Frullania-Radula-Porella* pioneer community, after the Hepaticae, mosses and lichens involved have formed a thick enough mat of organic material. In this case, the accumulation of organic material involves development of a layer that is more moisture-retaining, hence there is a distinct evolution towards a more mesic secondary society. On

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* This community occurs over most of the more exposed sites around Lake Superior, in the ravines running into it; I have studied it in Minnesota, Michigan, and Wisconsin. It recurs as an attenuated "disjunct" community, southward, in the deciduous region over shaded, dry, calcareous sandstone, as at Minneapolis—where the more subarctic species, however, are lacking.

Belle Rose I., Susie Islands, I have studied this succession, which is admittedly rather rare. Here *Frullania asagrayana* and *bolanderi* underwent ecesis, together with crustose lichens and *Peltigera*, etc., and such xeric mosses as *Hedwigia*, etc. Zonation from the more recently covered areas to the areas less recently covered showed distinct intergradation to a community formed by *Lophozia barbata, Lophocolea minor*, etc.

2. *Mesophyte Lophozia (Leicolea) heterocolpa-Blepharostoma-Tritomaria scitula-Odontoschisma macounii Associule.*—This community is characterized by the presence of one or more of the above index species. In addition, there is persistence of a number of species from the pioneer mesophyte *Leiocolea-Preissia-Scapania* community, among them chiefly: *Plagiochila asplenioides, Scapania mucronata*, rarely *Scapania cuspiduligera*. The pH of the thin layer of humus shielding the community from the basic underlying rock is generally about 5.4-5.8. Characteristic, if rare, associated species of this community are *Lophozia grandiretis, Tritomaria quinquedentata*, etc. At this point there is often ecesis of the more tolerant non-calciphiles, such as *Lepidozia reptans, Geocalyx graveolans, Cryptocolea imbricata*, etc., as well as persistence of such mosses as *Gymnostomum aeruginosum*.*

This community is of decided interest, since it occurs on the Susie Islands and at Grand Marais over horizontal or gently sloping ledges, where it forms a gradually accumulating peat layer (leading eventually to further succession to more xerophytic, oxylophytic communities). This subneutral peat layer serves as a matrix in which a number of interesting arctic-alpine vascular species undergo ecesis, among them: *Primula mistassinica* and *intercedens, Pinguicula vulgaris, Polygonum viviparum, Selaginella selaginoides*, and occasionally *Empetrum atropurpureum* and *E. nigrum*.

With the gradual accumulation of peat, the pH goes well below 5, and then we may get the ecesis of the *Mylia-Odontoschisma-Sphagnum* associule (p. 272). Under such conditions an anomalous consociation of the weakly basiphile *Lophozia heterocolpa-Blepharostoma-Tritomaria scitula-Odontoschisma macounii* and of the strongly oxylophytic *Mylia-Odontoschisma-Sphagnum* associule may obtain. A curious patchwork then results, showing microzonation from less acid to more acid sites. Furthermore, over the dead peat facies, such species as the very rare *Scapania carinthiaca* may undergo ecesis. This minute species, having a very low competition-coefficient, unable to compete with large species (such as *L. grandiretis*), is only a very temporary element, hanging on, so to speak, only because of its abundant gemmae production. Under such conditions we also get the very anomalous aggregation of the two related *Massula* species, *Lophozia (M.) grandiretis* and *L. (M.) incisa*, the former characteristic of subneutral sites, the latter a strong oxylophyte. Small quadrats of this advanced community were studied in detail on Belle Rose I., Cook Co., Minn., because of the very unusual aggregation of rare species. The following analysis (table 4) of eight small quadrats shows the great variation in the community, within an area 3 x 1 ft. in size. In addition

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* This community is very abundant and characteristically developed in the calcareous tundra of the high Arctic, as on the Arctic Ocean coast of Ellesmere Island. All four of the index species are present (although the *T. scitula* is replaced by an allied vicarious species), as well as *Lophozia quadriloba, Cryptocolea, Tritomaria quinquedentata*, etc.

to the basiphytic *Pinguicula* and *Primula intercedens*, the oxylophytic *Empetrum nigrum*, *Vaccinium vitis-idaea* var. *minus*, and *Potentilla tridentata* formed the vascular element undergoing ecesis.

Several distinct facies of this community (before the ecesis of the strongly oxylophytic species) may be distinguished. The following are perhaps the most interesting.

A. ODONTOSCHISMA MACOUNII-BLEPHAROSTOMA-LOPHOZIA GRANDIRETIS FACIES: Occurring frequently both on Big Susie I., and at Grand Marais. Usually the *Odon-*

TABLE 4.—Community analysis of a peat-covered bank, Belle Rose I., Susie Isls., Cook Co., Minnesota. (Size of plot indicated in square inches.)

Species	Plot No.							
	1 (6″)	2 (6″)	3 (4″)	4 (6″)	5 (3″)	6 (6″)	7 (6″)	8 (4″)
Lophozia grandiretis	5%	5%	25-30%	18-20%	85%	10%	......	......
Lophozia incisa	3	......	tr	2-3	......	......	30	......
Odontoschisma macounii	35-45	5-10	......	......	......	......	tr	45-50
Riccardia palmata	5-10	25-30	......	5-10	......	3-5	10	5-10
Blepharostoma trichophyllum	25-35	......	5	50-60	......	45-65	20-30	3
Lepidozia reptans	5	......	10	5	......	......	5	......
Lophozia heterocolpa	tr	......	tr	2	......	......	......	2-3
Geocalyx graveolans	8	......	15	......	......	5	......	......
Scapania mucronata	5-8	......	......	......	......	tr	......	......
Tritomaria exsectiformis	tr	......	tr	1	......	4-5	10	......
Mnium sp.	tr	......	tr	1	......	......	......	......
Odontoschisma denudatum	......	......	......	......	......	......	15	......
Scapania carinthiaca	......	0.1	......	......	2	5	......	tr
Cephalozia pleniceps	......	35-40	......	......	4-5	5	......	25-30
Dicranum sp.	......	5	......	......	......	......	......	......
Plagiochila asplenioides	......	......	25-30	......	......	......	......	......
Mylia anomala	......	......	......	1	......	......	3-5	......
Mosses	......	......	10	......	......	tr	......	......
Lichens	......	......	......	tr	......	......	......	......
Bare dead peat	......	10-15	......	......	5-8	5-10	......	15-20

toschisma is the dominant species, with a coverage of at least 5-60%. *Lophozia hetero-colpa* and rarely *Scapania cuspiduligera* are present as accessory species (as at Grand Marais). The *Scapania*, if present, usually persists from the more basic, initial stages of bare, moist rocks.

B. CRYPTOCOLEA IMBRICATA-SCAPANIA GYMNOSTOMOPHILA-TRITOMARIA SCITULA FACIES: Occurring on Porcupine I., Susie Isls., and on Isle Royale. Usually associated with several calciphilous mosses (*Fissidens osmundioides, Myurella julacea, Distichum capillaceum* especially), as well as with *Tritomaria quinquedentata* and *Lophozia hetero-colpa*. Usually with traces of the more ubiquitous *Blepharostoma*, as well as with *Plagio-chila asplenioides*.*

C. LOPHOZIA HETEROCOLPA-BLEPHAROSTOMA FACIES: Widespread, and often with impoverished, entire-leaved forms of *Plagiochila* consociated, as well as *Scapania mucronata*, occasionally *Tritomaria scitula* (as at the Gooseberry River).

II. *Invading over acidic or neutral rocks, the pH of the humus-layer less than 5.2. These communities represent advanced stages of the initial Sphagnum associule over wet cliffs and ledges, or of the various manifestations of the oxylophyte, mesic-xeric Lophozia-Scapania-Andreaea communities treated previously. Depending on whether the initial stage was hydrophytic or whether the initial stages were more xeric, different communities evolve.*

1. *Mylia-Odontoschisma-Sphagnum Associule.*—This community occurs under extremely acid conditions on the crests of cliffs, "capping" these cliffs where seepage is fairly constant, in areas where there is little direct sunlight (on the north or northwest facing crests of cliffs and ledges).† The most characteristic features of the community are its extreme oxylophyte nature (pH 3.7-4.4; eleven measurements), its constant association with the *Ledum-Vaccinium* heath, for which it serves as a matrix, and its extraordinary richness in species (both of Hepaticae and mosses; to a less degree of lichens). As with the other acid bog communities, the community is essentially a xerophyte community, in spite of the fact that, in most cases, one can wring water out of the moist or even saturated *Sphagnum*-matrix.

The community is extraordinarily similar to the *Mylia-Cladopodiella* associule of peat-bogs, and shares with it in common a large number of Hepaticae (*Mylia anomala, Calypogeia sphagnicola, Cephalozia media, C. loitles-bergeri*) and mosses (*Sphagnum* spp., *Polytrichum*, etc.) as well as vascular species (*Drosera rotundifolia, Ledum groenlandicum, Vaccinium vitis-idaea, V. oxycoccos*, etc.).

It is an unstable community and shows a certain amount of succession. On both Isle Royale and on the Susie Islands, there appears to be invasion originally (at seepage-wet points) by *Sphagnum*. On Belle Rose I., in 1948,

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* This community is very frequent on the Arctic Ocean coast of northern Ellesmere Island, where it was found repeatedly in 1955. The identical species occur, except that *T. scitula* is replaced by an undescribed vicarious species, and *P. asplenioides* is replaced here and there by *P. arctica*. In addition, *Odontoschisma macounii* (and sometimes also *Lophozia quadriloba, Anthelia juratzkana* and various mosses, most often *Distichum capillaceum, Myurella julacea* and *Drepanocladus* sp.), are associated in this community, on the Ellesmere Island coast.

† This community has been studied in great detail on the Susie Islands (where it is widespread on Long I., Belle Rose I., Big Susie I., Lucille I., Porcupine I., as well as on Amygdaloid I., Isle Royale (Michigan). The community was studied in detail in 1947-1948.

the writer denuded several quadrats, and then removed all of the peat, down to bed-rock; in one case as much as 10-12 in. deep. The surface (see Plot 3, below) consisted of an extreme xerarch community (Lichen-*Odontoschisma* facies of the *Mylia-Odontoschisma-Sphagnum* associule), which existed on the surface layer of the dead, underlying peat. All but the immediate surface-layer (1 in. or less) of this quadrat consisted of well-preserved remnants of pure *Sphagnum,* indicating that the *Sphagnum* was pioneer. There appears to be a decided successional pattern that can be elucidated: an initial *Sphagnum* stage, unaccompanied by other bryophytes; subsequent to the formation of a dense peat-layer (several inches deep or more) there is drying out of the surface; seepage will keep the bottom of the mat wet, but no longer the surface. Then the second community undergoes ecesis; the *Mylia-Odonto-schisma* facies appears. When the peat-layer becomes even thicker, and the surface, as a consequence, even more xeric, the final, xerarch community (Lichen-*Odontoschisma* facies) succeeds.* Correlated with this pattern of succession we find the gradual invasion of small vascular species (all woody and ericaceous, except for *Drosera rotundifolia*), especially *Vaccinium vitis-idaea, V. oxycoccos, Ledum groenlandicum,* as well as seedlings of spruce. With the gradual accumulation of peat, the *Vaccinium* heath becomes more dense, the spruces become larger, and *Betula papyrifera* and *B. cordifolia* undergo ecesis. The typical spruce-fir-birch forest thus eventually succeeds.

This successional pattern obtains ideally when the slope is not too great, or when the *Sphagnum* occurs on broken, step-like ledges: if the general slope is over 45°, the successional pattern stops before the attainment of the spruce-fir-birch forest. If the slope is over 65°, there is usually only partial succession to the *Vaccinium* heath.

The initial stages of this community therefore persist, in their most perfect development, on the steepest slopes (of over 75°), where succession normally goes through the Lichen-*Odontoschisma* facies (on the most vertical exposures), and through the *Hylocomium-Bazzania* facies on the crests, where more exposed conditions prevail. The smaller heaths (*Vaccinium* spp.) and *Drosera* undergo ecesis, but the larger types (*Ledum groenlandicum*) are absent or rare. At the juncture, therefore, with sudden steep declivities, we find the *Mylia-Odontoschisma-Sphagnum* associule persisting. Generally, at the very juncture with bare, exposed, seepage-moist rock, we find several species that are not typically part of the *Mylia-Odontoschisma-Sphagnum* associule, namely 1) a narrow zone of *Ptilidium pulcherrimum,* in thin mats; a pioneer species occurring here because of the adequate moisture, or 2) a *Lophozia attenuata* zone (often mixed with *Ptilidium pulcherrimum*), or 3) a *Gymnocolea-Cephalozia bicuspidata* associule. The latter, a pioneer on bare rocks, occurs here because of the extremely acid seepage and exposed nature of the matrix. (See p. 263 for this community).

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* This is the case on the steeper, more nearly vertical sides of the peat hummocks; on the upper portions of the peat hummocks we usually get succession, by the time the *Vaccinium* heath begins to be common, of a *Hylocomium-Bazzania trilobata* facies.

As the Vaccinium Heath succeeds, the Lichen-*Odontoschisma* stage is gradually replaced by a *Hylocomium-Bazzania trilobata* stage, always accompanied by various Cladoniae of the *rangiferina* group.

The *Mylia-Odontoschisma-Sphagnum* associule proper consists of three facies:

A. MYLIA-ODONTOSCHISMA FACIES: A community undergoing ecesis over the pioneer *Sphagnum* community, forming a thin stratum over relatively dry and nearly vertical peat slopes. The typical Hepaticae are *Mylia anomala, Odontoschisma denudatum* var. *laevissima, Calypogeia sphagnicola, Cephalozia media, Lophozia silvicola* (or *porphyroleuca*), occasionally *Riccardia palmata, Lophozia incisa, Lepidozia reptans; Polytrichum* is a common associated moss. *Drosera rotundifolia* and *Vaccinium vitis-idaea* are the common vascular species undergoing ecesis.

This community may be typified by the following representative 12 x 12 in. plots, studied on Belle Rose I. (August, 1948) (table 5).

TABLE 5

Species	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
Sphagnum	60-65%	6-8%	———	90-95%	1-2%
Odontoschisma denudatum	18-20	70-75	25-30%	———	45-50
Mylia anomala	2-3	8-10	1	1	1
Cephalozia media	2	1	———	2-5	1-3
Calypogeia sphagnicola	1	0.1	———	10-15[1]	———
Lophozia ventricosa s. lat.	1-2	2-3	———	1	2-5
Ptilidium pulcherrimum	2-3	3-5	1-2	———	1
Ptilidium ciliare	———	———	———	———	1-2
Mosses	1	———	———	3-5	1-2
Ledum groenlandicum	1	———	1	———	8-10
Spruce seedlings	1	———	———	———	———
Drosera rotundifolia	1-2	———	———	———	6-10
Polytrichum	1	1	1-2	1	1
Vaccinium vitis-idaea	3-5	1	———	6-8	6-10
Lichens	0.1	1-2[2]	62-65[3]	2-3[4]	———
Vaccinium oxycoccos	———	———	———	1	4-6

[1] Locally higher; locally less than 0.1%.
[2] *Cladonia* sp.
[3] About 60% a stringy, brown lichen; less than 1% a *Cladonia;* 2-3% a *Usnea*-like species.
[4] 1-2% crustose lichens, less than 1% *Cladonia* sp.
Also with *Ptilidium ciliare* (1-2%); *Riccardia palmata* (1-2%); *Bazzania trilobata* (0.1%); *Lophozia incisa* (95%); *Dicranum* species (1-2%).

B. MYLIA-LOPHOZIA-SPHAGNUM FACIES: A community of older, more horizontal peat crests, characterized by the absence of *Odontoschisma denudatum*. The characteristic species are *Mylia anomala, Lophozia ventricosa* and *silvicola, Calypogeia sphagnicola, Cephalozia loitlesbergeri, C. media, Cephaloziella subdentata,* occasionally *Lophozia incisa.*

C. LICHEN-ODONTOSCHISMA FACIES: A community of older, drier, vertical peat crests, with lichens covering most of the area, associated with *Odontoschisma denudatum, Polytrichum,* and relict plants of *Mylia, Cephalozia media.* This community also may occur on the drier, nearly vertical faces of cliffs, where there appears to have been no earlier *Sphagnum* stage; then succession occurs from a pioneer lichen stage, to the Lichen-*Odontoschisma* facies. Eventually there may be succession to a *Hylocomium-Bazzania trilobata* facies, which is the most nearly climax of the various local associules of the "Muscoid" layer.

AQUATIC COMMUNITIES

These include only a very limited number of species, growing as pioneers on wet rocks, where they are permanently or periodically submerged or submersed. Two evident communities appear distinguishable:

1. *Chiloscyphus-Porella pinnata Associule.*—Occurring over wet rocks (occasionally also dead branches, etc.) in streams. Most commonly the aquatic modifications of *Chiloscyphus pallescens* and *polyanthus* are found (as

in the streams of the north shore of Lake Superior), very rarely associated with *Porella pinnata*, a species that often occurs in streams where it is periodically submersed. Elsewhere, we find *Riccardia sinuata, Jubula hutchinsiae* subsp. *pennsylvanica*, occasionally *Scapania undulata* associated with these species. In the mountains, elsewhere, a distinct *Scapania undulata-Marsupella sphacelata* associule occurs under similar conditions, locally replaced by the following facies.

2. *Scapania undulata-S. nemorosa Facies.*—Occurring on the vertical rockwalls of islands (especially Belle, Rose, Porcupine, and Big Susie I.) as pioneers, in a closed association which evidently totally lacks the power to undergo succession. The society is limited to the wave-action zone, from 0-24 in. above the level of Lake Superior; this is evidently a local faciation of the more montane *Scapania-Marsupella* community of rocky stream beds and waterfalls. Both of these are treated as local variants of the *Lophozia-Scapania* associule (see p. 267).

EPIPHLOEMIC AND EPIXYLIC COMMUNITIES

A large variety of species occur associated with the bark of living trees (corticolous or epiphloemic communities), or on the firm to decaying wood (xylem) of fallen trees (xylicolous or epixylic communities). The communities over bark show only a limited amount of succession (see the papers by Pessin, 1925 and Quarterman, 1949, on this); they are related most closely to communities formed by xerophyte pioneers over exposed rocks, the two areas sharing largely an identical associule (the *Frullania-Radula-Porella* associule, defined in Schuster, 1949). The communities over logs show a much closer relationship to the humicolous and helophytic communities than to the epiphloemic communities. As decay of the substrate proceeds, there is very evident succession from a group of evidently pioneer species, to species (such as *Bazzania trilobata*) that are frequent in the climax forest. It is, therefore, patently obvious that the present series of communities cannot be kept clearly apart from the pioneer, epipetric communities, on one hand, or the advanced humicolous communities, on the other hand.

EPIPHLOEMIC (CORTICOLOUS) COMMUNITIES

The communities of essentially pioneer nature that occur on the bark of living trees are related, on one hand, to the epiphyllous communities of the tropics, on the other hand, to the pioneer xerophytic communities of rockwalls. In an evolutionary sense, it is very probable that the following pattern occurred: epipetric communities→epiphloemic communities→epiphyllous communities. This appears to be indicated also by the fact that in general the species found in the epipetric *Frullania-Radula-Porella* communities are less phytogenetically advanced and include fewer highly modified Lejeuneaceae, than the corticolous societies. In turn, the purely epiphyllous societies of the tropics include the most extremely specialized and modified of all the Hepaticae, and one gets the impression that this community evolved from the corticolous types.*

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* Although epiphyllous communities are absent regionally, they occur northward to northern Florida. The Floridian epiphyllous species, and their "hosts," are reviewed in Schuster and Anderson (1955).

The writer would class all of the variations (extremely numerous in the tropics) of pioneer species, with a lobulate type of leaf, of either bare rock-walls, bark of trees, or leaves, as derived from a single basic associule.

1. *Frullania-Radula-Porella Associule.*—Widespread over the bark of trees, wherever there has been succession to a subclimax or climax forest (e.g., where moisture and humidity conditions have become high, and where a relatively dense shade occurs). The community is essentially xerophytic, but shows a certain amount of variation, depending on shade and humidity; in addition, there is a certain amount of internal succession, which has not been studied sufficiently locally.

The following local facies may be distinguished.

A. FRULLANIA FACIES (xeric extreme): Formed by several species of *Frullania* (chiefly *eboracensis, bolanderi*, more rarely *brittoniae, oakesiana*); rarely *Porella platyphylloidea* is associated, and sometimes forms a virtually pure consociation.

B. FRULLANIA-RADULA FACIES (less xeric): Formed largely by the above species of *Frullania*, with *Radula complanata* (rarely *Lejeunea cavifolia*) associated.

C. RADULA-LEJEUNEA FACIES (nearly mesic): Occurring over shaded bark, especially in *Thuja* swamps, where *Radula complanata* and *Lejeunea cavifolia* are consociated, occasionally with *Frullania bolderi* and *oakesiana* (rarely *selwyniana*, usually in calcareous areas).

D. COLOLEJEUNEA FACIES (extreme mesic): Occurring over densely shaded bark, sometimes of white cedar, more rarely over the shrub, *Taxus canadensis* (see Conard, 1945), in dense cold forests that are underlain by basic rocks (with presumably a high calcium content in the bark); formed by *Cololejeunea biddlecomiae*, occasionally associated with *Lejeunea cavifolia*, and (elsewhere) *Metzgeria furcata* and *Microlejeunea ulicina*, as well as *Frullania asagrayana* (which latter is nearly confined to rocks regionally).

E. FRULLANIA ASAGRAYANA FACIES (mesic-xeric): Over bark, particularly yellow birch. Although not known from bark in Minnesota, it is frequent on bark in Michigan (Deer Lake; Isle Royale); why this species should so often occur in almost pure consociation is not known.

Except for the *Frullania* faciations, the other forms of the *Frullania-Radula-Porella* associule are very infrequent locally; these faciations represent the attenuated extreme of the very polymorphic, tropical, *Lejeunea-Frullania-*rich associules of this same basic type. The following local epiphloemic associule, however, appears to be of distinctly boreal relationships.

2. *Ptilidium pulcherrimum Associule.*—Over the bark and branches of old spruce or fir trees, in the old climax forests, especially in the northeastern corner of the state, we very often find *P. pulcherrimum* forming the only epiphytic hepatic community present. Though relatively scarce locally, the *P. pulcherrimum* associule of coniferous bark is extraordinarily common in the "Hudsonian" Zone (e.g., upper edge of the boreal coniferous forest) in montane areas, such as on Mt. Washington, as well as in some areas of the Appalachian Mountains.

As with the *Frullania-Radula-Porella* associule, the present associule also occurs indiscriminately over somewhat dry rocks, as a pioneer.

EPIXYLIC (XYLICOLOUS) COMMUNITIES

Upon the decortication of a dead tree, the exposed xylem forms a fresh surface, upon which the ecesis of various faciations of a pioneer community occurs. In the temperate and boreal regions of the northern Hemisphere, this

appears to be very commonly formed by variations of the following associule (Schuster, 1949).

1. *Nowellia-Jamesoniella Associule.*—This associule is named after the two most common of the initial species, occurring throughout the coniferous and upper deciduous regions. Depending on light and moisture conditions, a great degree of variation occurs in the composition of the communities we get on decaying logs (see table I, p. 212), but at least three distinct pioneer (or near pioneer) facies appear distinguishable.

A. PTILIDIUM PULCHERRIMUM FACIES: Consisting of this single species, sometimes with lichens; occurring as a pioneer under the most xeric and sunny extreme; grading into the next. Often this strictly pioneer associule undergoes succession into the next, as the logs disintegrate, become more water-retaining, and more mesic conditions obtain.

B. NOWELLIA-JAMESONIELLA-PTILIDIUM FACIES: Under somewhat more mesic conditions than above, *Nowellia* and *Jamesoniella* also undergo ecesis, often accompanied by the ubiquitous *Lophocolea heterophylla,* occasionally by *Tritomaria* (*exsectiformis,* more rarely *exsecta*), *Anastrophyllum hellerianum, A. michauxii, Odontoschisma denudatum;* much more rarely by *Lophozia ascendens, L. porphyroleuca, L. longidens, Lepidozia reptans, Blepharostoma trichophyllum, Calypogeia suecica.* The latter 10 species usually (but not always) undergo ecesis somewhat later, after disintegration of the log has proceeded slightly further.* More careful study may result in the separation of this facies into two, related successionally. Under more mesic, usually much more shaded, conditions the following facies occurs. Often, the present associule will occur on the sunny, upper side of a log, while the following facies will occur on the shaded, north- or west-facing side. To a certain degree there is also some internal succession from the *Nowellia-Jamesoniella-Ptilidium* to the following facies.

C. CEPHALOZIA-RICCARDIA FACIES: Over moist, sheltered logs, either on the shaded sides of a log, or (in bogs and swamps) over the entire log, a very different facies of the *Nowellia-Jamesoniella* associule occurs. The two index species that give the associule its name become rare or occasional, and are replaced largely or entirely by more mesic species, chiefly the following: *Cephalozia media* and *C. catenulata,* more occasionally *C. lacinulata, C. macounii, C. pleniceps, C. connivens, Riccardia latifrons* (very rarely *R. multifida* and *R. pinguis* near marl bogs, or *R. palmata*), *Scapania glaucocephala, S. apiculata, Lepidozia reptans, Blepharostoma, Tritomaria exsectiformis* (more rarely *T. exsecta*), *Calypogeia suecica* and occasionally *C. meylanii, Lophozia incisa,* more rarely *L. ascendens.*

D. LOPHOZIA ASCENDENS FACIES: A rare and rather local phase, occurring largely in montane regions (frequent, for example, in the New England mountains), but rare locally. Associated are most of the preceding species, particularly often *Anastrophyllum hellerianum* and *Lophozia porphyroleuca* (see table 1, p. 211).

In many cases, at least, facies A (*Ptilidium* facies) will undergo succession to facies B (*Nowellia-Jamesoniella-Ptilidium*), more rarely perhaps to C. Facies B very frequently shows intergradation, or succession, to facies C (*Cephalozia-Riccardia* facies). In turn, as facies B and C mature, their activity, together with that of fungi, Mycetozoa, bacteria, the penetration by roots of vascular plants, etc., results in a disintegration and loosening up of

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* This community is extremely widespread on decaying logs, extending southward in the Appalachians to North Carolina. For example, on Andrews Bald, near Clingmans Dome, N. C., I have found this community on fir logs, the dominant species being *Nowellia curvifolia* and *Cephalozia catenulata,* with a cover of over 40 and 25% respectively. Locally *Jamesoniella* has a cover of 20-25%. Accessory species are *Riccardia palmata, Calypogeia suecica, Anastrophyllum michauxii,* accompanied by a trace of *Tritomaria exsecta.*

the decaying xylem. As rotting proceeds, and more mesic conditions obtain, the more delicate species (*Scapania, Cephalozia,* etc.) are succeeded by coarser, more robust species. The preponderance of relatively delicate Hepaticae in the earlier seral stages is gradually diminished, until mosses, chiefly pleurocarpous, as well as a few acrocarpous mosses, especially *Dicranum* and *Georgia* [*Tetraphis*], succeed. We then get the following humicole subclimax associule.

2. *Bazzania-Blepharostoma-Lepidozia Associule.*—Occurring over much disintegrated, moist decaying wood, as well as over rich humus. The three index species (*Bazzania trilobata, Blepharostoma trichophyllum, Lepidozia reptans*) are accompanied by *Geocalyx graveolans,* occasionally *Calypogeia meylanii, Lophozia incisa,* the ubiquitous and persistent *Lophocolea heterophylla,* more rarely by *Plagiochila asplenioides.* These Hepaticae are accompanied by *Tetraphis, Dicranum,* and many other mosses, and (except for the *Bazzania*) gradually lose out in competition to the more robust mosses. The basic history of each individual decaying log shows decided variations on this pattern, and the following individual facies can be easily found, as well as probably others.

A. TETRAPHIS-BAZZANIA-CEPHALOZIA MEDIA FACIES (mesic): Over relatively dry, but shaded decaying logs in acid woods. The *Cephalozia media* evidently merely persisting from facies C above. (Example: NW of Wyoming).

B. BAZZANIA-DICRANUM SCOPARIUM-FLAGELLARE FACIES (xeric): Over dry but relatively shaded logs, forming a very dense growth; on such well-decayed logs, such small vascular plants as *Lycopodium annotinum* often establish themselves. (Example: At Pigeon Point.)

C. CALYPOGEIA MEYLANII-GEOCALYX GRAVEOLANS-TRITOMARIA EXSECTIFORMIS-LOPHOZIA INCISA-MNIUM PUNCTATUM FACIES (hygric): Over decaying logs on wet, springy slopes, as at the Cascade River, and on Isle Royale.

Of the numerous other facies seen, most consisted largely or entirely of mosses, so are not mentioned here. Whatever the nature of this stage, it represents the evident subclimax stage, before the climax Moss-*Bazzania* Associule takes over (see under humicole associations).

HUMICOLOUS SOCIETIES

As succession proceeds we arrive at a stage where the forest floor of the coniferous regions attains a high level of uniformity. As stressed elsewhere (Schuster, 1949; p. 248 in this work), as we approach climax conditions, the Hepaticae nearly or quite drop out. For that reason, we may deal with the few strictly humicolous associules which we get in the subclimax, and the apparently largely single associule we get in the mature climax forest, in the following very simple terms.

It should be remembered, that these humicolous associules represent the advanced seral stages of various successional tendencies, ("serules") outlined in previous sections. For instance, over ledges, the pioneer *Ptilidium pulcherrimum* associule gives way to some faciation of the later *Scapania-Lophozia* associule, which, on developing a thick enough peaty layer (consequent upon growth, decay of the older portions, and periodical accumulation of a thicker

and thicker underlying organic matrix) succeeds to a *Mylia-Odontoschisma-Calypogeia* community. This in turn, after developing a thick enough peaty layer under it, may show succession to a *Dicranum-Bazzania-Sphagnum* community, which represents either the climax within the unistratal series we deal with, or is extremely close to it. In all cases, the Hepaticae are now competing against the mosses on very unequal terms, and are being rapidly eliminated.

SUBCLIMAX HUMICOLOUS COMMUNITIES

1. *Plagiochila-Riccardia-Moerckia Community.* — Over wet to saturated humus, in the basic *Thuja*-fir-spruce forests, usually in depressions or holes. *Plagiochila asplenioides* is accompanied by *R. pinguis* and *R. multifida* (perhaps rarely *R. sinuata*), and by *Moerckia hibernica*; this is a hygrophytic associule, related to the marl bog associules to be described later (p. 282).

2. *Calypogeia-Scapania irrigua-Geocalyx Associule.*—An analogous associule of more acid, boggy spruce-tamarack forests (as near Hoveland), where the mesic climax conditions do not yet obtain.

3. *Lophozia incisa-Lepidozia-Bazzania trilobata-Sphagnum Associule.*—An associule of wet, peaty areas, in subclimax (occasionally, secondarily, open climax forests).

The above three associules from over moist humus are examples of only three intermediate successional stages, from the ledge, bog, log seres which are outlined at some length. Several other communities occur under moist subclimax conditions in coniferous forest; as the climax is attained, however, the Hepaticae are virtually eliminated, and the following associulé results.

CLIMAX HUMICOLOUS COMMUNITY

1. *Hylocomium splendens-*(*Calliergon schreberi*)-*Bazzania trilobata Associule.*—This associule occurs under the oldest spruce-fir forests, which have not been disturbed, except where accumulation of needles is so dense that the entire moss-carpet is eliminated. The associule is dominated by *Hylocomium*, as well as by other large pleurocarpous mosses, such as *Ptilium crista-castrensis*, *Hypnum* spp. *Calliergon* spp., under somewhat xeric conditions often by *Dicranum*, while *Sphagnum* may persist for long periods under moist conditions (even under very old virgin forests, as on the Susie Islands). Associated with these mosses, we find a dense growth of various species of *Lycopodium*, of *Vaccinium uliginosum* and *vitis-idaea*, but very few other vascular plants. The only species of Hepaticae which persists into such climax forests, appears to be *Bazzania trilobata*. Forests of this type are well developed on many of the Susie Islands, where disturbance has been very slight, and where the ground moss-mat is particularly well-developed because of frequent mists and fogs. Under such conditions, in the climax, the epiphytic species usually drop out, except for the lichen *Usnea*, and similar species.

HELOPHYTIC (SWAMP AND BOG) COMMUNITIES

In swamps, and particularly in bogs, we have a series of successions which are particularly well-known. The recent paper by Conway (1949) should be consulted here, though it does not apply to all of the northeastern

bogs. The pattern of succession among the Hepaticae has been recently discussed by the writer (Schuster, 1949). The following treatment applies not only to the region dealt with herein, but also to much of the boreal regions of the entire Northern Hemisphere.

In the coniferous panclimax, the following successional pattern, among the vascular plants, appears to generally obtain; this serves as a pattern upon which the successional patterns of the Hepaticae (and mosses) may be superimposed. It should be noted that two very different seres occur, depending on whether the initial stages occur in a marly or in an acid lake or pond. As with other calciphile successions, the gradual secretion of organic matter by the plants usually results in a gradual approach to the oxylophytic sere.*

CALCIPHILOUS SERE

This occurs scattered in the bogs near the north shore of Lake Superior, where the underlying rocks are basalt, or rove-slate, and in much of the area from Lake Itasca north to Lake of the Woods (the old "Lake Agassiz"). Ideally, we get at least five stages in succession, from open water until the subclimax. In some cases, instead of getting a *Chamaedaphne* heath, an alder-willow swamp may result. Typically, the pattern (based to a large degree upon very detailed studies at Grand Portage, and somewhat less detailed ones under subclimax conditions at Lake Itasca, and at Lake of the Woods) may be outlined as presented below (table 6).

1. *Utricularia intermedia-vulgaris associule of open, shallow, marl bog pools.*—Typically, no Hepaticae are found in this stage, though at the very edge of the open water, amidst *Sparganium minimum, Triglochin palustris, Drosera intermedia, Moerckia hibernica* and *Riccardia pinguis* (as at Grant Portage) may occur.

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* Furthermore, locally in marl bogs the accumulation of peat may be great enough so that even in the open bog stage, oxylophytic communities may come in. For instance, in the marl bog at Grand Portage, subsequent to the formation of *Sphagnum*-moss tussocks 12-18 in. above the marly water, the *Mylia-Cephalozia-Calypogeia sphagnicola-Cephaloziella subdentata* community underwent ecesis, though this never occurs under even slightly marly conditions. Furthermore, not three feet from this community was a "subcalciphile" *Lophozia grandiretis-L. schultzii* community, typical of how succession thus is always modified by local conditions.

This progression from basic or marly central lake, to acid, peaty, bog vegetation is also clear from the studies of Conway (1949, p. 178), who gives a mean pH of 6.94 for the lake water of Cedar Creek Bog (Anoka Co.); the surrounding pioneer "sedge" mat consists largely of *Decodon verticillatus* and *Typha latifolia*, with the pH mean at 6.53. In this occur only two Hepaticae, both very lime-tolerant, *Riccardia pinguis* and *Marchantia polymorpha*. In the surrounding *Thuja* forest the pH varies from 6.39 mean (5.03-7.12 range) in some plots to a low of 4.26 (where *Sphagnum magellanicum* was growing). Under the latter condition, with the *Sphagnum*, the writer has found associated the oxylophytic Hepaticae, *Cephalozia media, connivens* and *pleniceps, Odontoschisma denudatum, Cephaloziella elachista* (with pH varying from 3.6-4.1). Associated vascular plants are *Drosera rotundifolia, Chiogenes hispidula, Vaccinium oxycoccos, Ledum groenlandicum*.

Conway also makes the very valid observation that there is no sharp separation between the acid bog succession, and between bogs starting from marly lakes ("marl bog succession"). Therefore, in intermediate bogs, an integradation must be expected between the two following serules depicted.

TABLE 6.—Idealized successional pattern for helophytic communities

"Calciphilous" Sere	"Calciphobous" Sere
Open marl bog	Open acid pond
↓	↓
(*Utricularia* associule)	(*Utricularia* associule)
↓	↓
Scorpidium-sedge mat ――――――→	*Sphagnum*-sedge mat
↓	↓
Chamaedaphne heath	*Chamaedaphne* heath
(or *Cornus-Alnus-Larix* scrub) ――――――→	Black spruce-tamarack
↓	swamp forest
Arbor-vitae swamp ↓	
(Usually subclimax)	(Usually subclimax)
――――――→ Spruce-fir climax forest ←――――――	
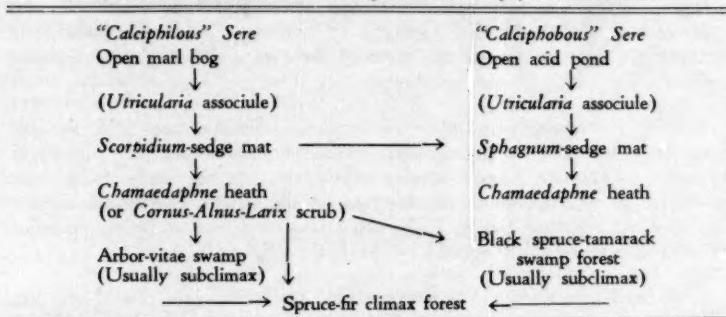
2. *Scorpidium-sedge mat stage.*—Analogous to the *Sphagnum*-Sedge Mat of the "calciphobous" sere. The dominant bryophyte is often the large, bronzed conspicuous moss, *Scorpodium scorpioides*, more rarely a *Drepanocladus*. No woody plants occur as yet, but such vascular plants as the marl plants *Eleocharis elliptica*, *Triglochin palustris* and *Parnassia palustris neogaea* may occur, as well as the very tolerant *Drosera rotundifolia* and *D. intermedia*, *Scirpus hudsonianus* and *Rhynchospora alba*. Among the Hepaticae which undergo ecesis during this stage are two very typical ones, usually of rare occurrence, *Lophozia schultzii* (*Leiocolea rutheana*) and *Moerckia hibernica*, as well as the more widely distributed, lime-tolerating *Riccardia pinguis*, and the usually epipetric *Preissia*, occasionally large forms of *Chiloscyphus pallescens*.*

3. As organic matter accumulates, slightly lime-tolerating species of *Sphagnum*, especially *squarrosum* and *subsecundum*, may undergo ecesis; we may then get the succession of a *Sphagnum*-sedge mat somewhat similar to that of the oxylophytic bog succession. However, the Hepaticae are largely quite different. *Mylia anomala* is rare or absent; *Cladopodiella fluitans* is quite absent. On the other hand, the somewhat lime-tolerating *Scapania irrigua* and *S. paludicola* become frequent. Perhaps most characteristic, at this stage, *Lophozia grandiretis*, a very rare but characteristic species, undergoes ecesis, while *Lophozia schultzii* and *Moerckia hibernica* persist from the preceding stage. The common marl-bog species, *Riccardia multifida* also undergoes ecesis, and *Riccardia pinguis* remains a frequent accessory species. *Calypogeia meylanii* undergoes ecesis at this point in succession, and elsewhere, we find *Microlepidozia setacea* commonly undergoing ecesis at this stage.

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* The above represents the conditions in the bog at Grand Portage. Under less boreal conditions, as for instance, in the bog at Cedar Creek, Anoka Co. (actually within the Deciduous Forest Region), there is no such sedge mat, and no *Scorpidium*—this stage being formed partly by *Typha latifolia*, partly by *Decodon verticillatus*, with such mosses as *Drepanocladus aduncus* var. *kneiffii*, and such sedges as *Carex lasiocarpa*. *Drosera* is absent, but *Sarracenia purpurea* occasional, while the "calciphilous" bog plant, *Menyanthes trifoliata* is occasional.

As conditions get much more acid, the Hepaticae of the crests of the *Sphagnum* hummocks also undergo succession, with the lime-tolerating species dropping out, while a *Mylia-Calypogeia sphagnicola-Cephaloziella subdentata* community (characteristic perhaps more of the next stage) begins to undergo ecesis.

4. *The Chamaedaphne Heath.*—As conditions become more acid, shrubby plants begin to come in, among them commonly *Chamaedaphne, Vaccinium oxycoccos,* occasionally *Cornus* species, *Alnus,* etc. In the shade under these shrubs, we get the maximum development of the strictly oxylophytic *Mylia-Cladopodiella* associule (see p. 285), often associated with an index species of the preceding more marly conditions, *Scapania irrigua.*

5. *Arbor-Vitae Swamp Subclimax.*—The *Mylia* associule now drops out, with the forest floor largely taken over by mosses. In depressions or holes, however, we may find locally development of the subclimax associules described for the humicolous communities, namely, the *Plagiochila-Riccardia-Moerckia* associule, as well as in less marly areas the *Calypogeia meylanii-Scapania irrigua-Geocalyx* associule. Over decaying logs, which first make their appearance here, the various epixylic associules (p. 277) now appear, and on the bark of arbor-vitae we usually get the relatively mesic *Frullania-Radula* facies, of the *Frullania-Lejeunea-Porella* associule (see p. 276).

The subclimax stage has been studied in detail both at Grand Portage, as well as at La Salle swamp, adjacent to Itasca Park, Minn. At the latter locality, in an advanced stage, with dense forest cover (*Thuja* as a relict tree; *Abies* becoming frequent) an approach to the climax obtains, and on the forest floor we get relicts of the preceding stages. The communities of the forest floor are virtually all humicolous (see p. 279 for their description). On relatively mesic humus, facies of the *Calypogeia meylanii-Scapania irrigua-Geocalyx* associule occur, lacking the *Scapania* (which always appears to drop out with approach to the climax). Rarely associated is *Cephalozia media,* more rarely still, traces of *Mylia anomala* (both persisting from the *Chamaedaphne* heath stage). In wet holes, around small pools and springy places, the *Plagiochila-Riccardia-Moerckia* associule occurs, occasionally with the ubiquitous *Lophocolea heterophylla;* the *Riccardia* represented by *R. multifida* and *R. pinguis.*

The various serules of this succession have been studied in most detail at Grand Portage Bog, where the community is developed to its maximum extent. Here we find, depending on local conditions, succession from the *Scorpidium*-sedge mat to either a *Chamaedaphne* heath (with very acid, strongly insolated conditions), or a distinct *Cornus-Alnus* shrubby stage, often with *Larix* associated, occurs. The former almost inevitably shows succession to an arbor-vitae stage. The latter may show succession to this stage, or (more commonly) shows succession directly to the spruce-fir climax forest. This is clearly indicated by the above diagram. The various bryophyte communities (selected to show maximum representation of Hepaticae) are analyzed below (based on study of 12 in. square plots).

PLOTS 1-2.—Sunny, wet exposed, marly muck, at edge and less than 6 in. above level of open water (Plot 1), or on low, wet, strongly insolated marly peat (Plot 2). This plot corresponds well to the latter stages of the *Utricularia* associule outlined above.

	Plot 1	Plot 2
Riccardia pinguis	10-14%	30-40%
Moerckia hibernica	8-12	20-30
Drosera intermedia	25-30	25-30
Carex, Triglochin		
palustris, etc.	20-35	————
Bare muck	*ca.* 20	30
Utricularia intermedia	trace	————

PLOTS 3-4.—*Scorpidium*-sedge mat stage: bryophytes partly shaded by *Carex* sp., but no shrub or tree cover.

	Plot 3	Plot 4
Scorpidium scorpioides	70-80%	25-30%
Preissia quadrata	10-15	trace
Riccardia pinguis	10-15	10-15
Lophozia schultzii	trace	15-20
Moerckia hibernica	————	20-25
Other mosses (chiefly		
Drepanocladus)	————	<5

PLOT 5.—Wet, hygric, shaded community, back from *Scorpidium*-sedge mat (in narrow *Cornus-Thuja* zone, between sedge-mat and more elevated spruce-fir forest); corresponding nearly to the *Cornus-Alnus-Larix* stage. (Bryophytes forming matrix for ecesis of *Menyanthes trifoliata*.)

Lophozia schultzii	20-25%	*Riccardia multifida*	1%
Riccardia pinguis	2-5	*Sphagnum*	5-8
Pellia epiphylla	1-2	Mosses (*Scorpidium*;	
Moerckia hibernica	5-7	*Drepanocladus*, etc.) 55-65	

PLOTS 6-7.—Juncture of *Thuja* subclimax forest and open *Scorpidium*-sedge mat stage (with *Chamaedaphne* heath scarcely developed); plots situated on somewhat peaty crests of *Sphagnum*-moss polsters, at base of which open, somewhat marly water occurs. In herb layer, *Smilacina trifolia*, *Drosera rotundifolia*, *Rubus* (?*flagellaris*), *Carex* sp., *Vaccinium oxycoccos*, *Eriophorum virginicum*. Plot 6, from a low polster, showing little zonation. Plot 7, from a high polster, showing zonation from a lower zone (bottom 3 x 12 in.) in which *Moerckia* and *Riccardia* predominate, to a median 3 x 12 in. zone, where the less basiphyte *Lophozia grandiretis* and *Cephalozia pleniceps* predominate, to an upper, oxylophytic 3 x 12 in. zone in which *Mylia*, *Calypogeia sphagnicola* and *C. meylanii* occur in traces (among *Sphagnum*), foreshadowing the more oxylophytic communities.

	Plot 6	Plot 7	
Lophozia schultzii	25-30%		
Riccardia multifida	15-18	1-2%	} Lower 25%
Moerckia hibernica	3-5	18-24	of plot
Lophozia grandiretis	————	30-35	
Cephalozia pleniceps	————.	3-5	} Middle 35%
Drepanocladus sp.	25-30	————	of plot
Sphagnum sp.	6-8	4-8	
Thuyidium sp.	<2	————	
Hylocomium sp.	<2	————	
Other mosses	<5	25-30	
Calypogeia meylanii	————	<1	} Upper 40%
Calypogeia sphagnicola	————	trace	of plot
Mylia anomala	————	1-2	
Bare (dead) peat	<1	10-12	

PLOTS 8-9.—Wet, exposed, sunny, strongly elevated polsters (2-2.5 ft. above water level); plot 8 at juncture of heath and *Thuja* subclimax; plot 9 in *Chamaedaphne* heath, at base of old *Larix* stump. Associated vascular plants: *Ledum groenlandicum, Vaccinium oxycoccos, Drosera rotundifolia, Trientalis borealis*. Forming typical *Mylia-Cephalozia* facies (of *Mylia-Cladopodiella* associule).

	Plot 8	Plot 9
Mylia anomala	20%	25-30%
Sphagnum sp.	60	8-9
Cephalozia pleniceps	<5	8-10
Calypogeia sphagnicola	<2	16-20
Cephalozia loitlesbergeri	<1	<3
Riccardia (?*latifrons*)[1]	2-5	6-8
Mosses	8-10	<2
Cephaloziella subdentata[2]	<0.1	<0.1
Dicranum sp.	2-5	8-10
Lophozia grandiretis[3]	——	trace
Geocalyx graveolans[2]	——	<2
Blepharostoma trichophyllum[2]	——	trace

[1] The *Riccardia* possibly *R. palmata*, but not definitely determinable.
[2] Locally in small patches; then with coverage up to 60%.
[3] Remnants of the earlier seral stages; barely remaining as traces near the lower (least oxylophytic) edges of the quadrat.

OXYLOPHYTIC SERE

This occurs in bogs where there is a slight or no trace of lime in the underlying soil, where therefore the bog-waters that represent the initial stages, have a pH consistently (and usually well) below 5.0. Under very slightly basic conditions (usually to be noted by the presence of the index species, *Thuja occidentalis*), transition to the foregoing seral stages, of course, is to be expected.

1. *Open Acid Pond—Utricularia Associule.*—Usually no Hepaticae occur at this point, where various *Ultricularia* species occur (*cornuta, intermedia, vulgaris,* etc.) though the aquatic form of *Cladopodiella fluitans,* rarely sub-aquatic forms of *Pellia epiphylla,* occur (as at bog at Kerrick, with pH *ca.* 5-4.3).

2. *Sphagnum-Sedge Mat.*—At this point we find ecesis of the *Mylia-Cladopodiella* Associule (see Schuster, 1949, p. 142). Such sedges as *Eriophorum spissum* and *E. virginicum* and *Rhynchospora alba* occur with such vascular plants as *Vaccinium oxycoccos* and *Drosera rotundifolia* and *Sarracenia purpurea,* in a matrix of *Sphagnum.** Forming a thin mat over the *Sphagnum,* we find a layer society dominated usually by *Mylia anomala* (which may be so robust as to form pure mats several feet across, killing the *Sphagnum* beneath it), with the following accessory species: *Calypogeia sphagnicola, Cephaloziella elachista,* rarely *C. rubella, Cephalozia media, C. loitlesbergeri, C. connivens, C. compacta, C. pleniceps,* occasionally *Lophozia*

* As already noted under the Epipetric Communities (p. 272) this associule also occurs in modified form (the *Mylia-Odontoschisma* facies) over *Sphagnum* at the crests of peat-covered ledges. There we find the same species of *Cephalozia,* but find the *Cephaloziella elachista* replaced by *C. subdentata,* the *Lophozia marchica* replaced by *L. incisa,* and the *Cladopodiella* replaced by *Odontoschisma denudatum.*

marchica or *L. capitata*. The pH of this sedge mat-*Sphagnum* stage is *ca.* 4.3 (at Kerrick) or may even go down to 3.6 or lower.*

The *Mylia-Cladopodiella* associule, usually growing in mats over *Sphagnum*, occurs in several facies, three of which are perhaps most easily distinguishable.

A. MYLIA-CLADOPODIELLA FACIES: Usually occurring in the wettest portions of the bog (and becoming rare in mature *Chamaedaphne* heath, in most cases). *Lophozia marchica* is often consociated, but the *Cephalozia* species usually do not come in until moisture conditions become less extreme. In bog holes, subject to seasonal submergence, a *Cladopodiella* consociation may occur. *Cephaloziella elachista* is often present (and binds the facies to the next one).

B. MYLIA-CEPHALOZIA-CEPHALOZIELLA FACIES: Characterized by the absence of *Cladopodiella*. This community is much more frequent in regional bogs, in which the *Cladopodiella* is quite rare. The *Cephaloziella*, under moist conditions, is almost uniformly *C. elachista;* under relatively xeric conditions (as at Grand Portage), *C. subdentata* may occasionally replace it. *Cephalozia pleniceps, C. loitlesbergeri, C. connivens* (and the dubiously distinct *C. compacta*) are the commonly associated *Cephalozia* species. *Lophozia marchica* (more rarely *capitata*) occurs occasionally.

C. MYLIA-SCAPANIA IRRIGUA (PALUDICOLA) FACIES: Characteristic of bogs with traces of underlying marly soil or peat, in which the pH is usually not as extremely low as in A and B (above). Usually with *Cephaloziella elachista* absent, and never with *Cladopodiella* present; the more tolerant *Cephalozia* species are always present.

3. *Chamaedaphne Heath.*—In addition to *Chamaedaphne*, such ericaceous plants as *Kalmia polifolia, Vaccinium oxycoccos, Ledum groenlandicum* become common. The *Mylia-Cladopodiella* associule persists, but several species of less boggy conditions come in, among them occasionally *Lophozia ventricosa, Riccardia pinguis*, bog forms of *Ptilidium ciliare,* etc. The pH is comparable to that obtaining above.

In a poorly developed *Chamaedaphne* heath, south of Ham Lake, Anoka Co., near the southern edge of this type of community, a completely aberrant hepatic community has been observed over peat. This may be the result of pasturing and partial clearing. The Hepaticae included *Lophozia capitata, Pellia epiphylla, Lophocolea heterophylla, Cephaloziella rubella sullivantii,* and *Fossombronia foveolata.* The pH at the site (among the *Fossombronia*) was 4.7 to 5.0. Associated vascular plants were *Xyris torta, Drosera rotundifolia* and *longifolia, Lycopodium inundatum, Calopogon pulchellus, Vaccinium oxycoccos, Oenothera fruticosa, Carex* sp.

The site is of decided interest in that it is an example of the "dry bog" extreme, due partly to the "dry thirties" when rainfall averaged far below the norm (see discussion in Conway, *loc. cit.*), partly to drainage. A very similar (but undrained) *Chamaedaphne* heath, studied 3-4 miles north of Hinkley, Minn., also showed the consociation of *Lophozia capitata* and *Lophocolea heterophylla,* together with mosses (among which *Sphagnum* was a rare element). The *Chamaedaphne* heaths, in the Jack-pine barrens of Michigan (in which *Lophozia capitata* is so common), also belong probably to this "dry bog" community. See p. 287 for discussion.

4. *Black Spruce-Tamarack Forest.*—With succession of the subclimax forest we find the *Mylia-Cladopodiella* associule largely or totally eliminated. The

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* A somewhat similar, analogous successional stage is formed by the *Eriocaulon-Juncus*-sedge mat around the edges of sandy, acid lakes, as at Deer Lake, Michigan. Such sandy moors appear to be absent (or at least very rare) locally. Here we find associated with *Drosera* spp., and *Xyris* and *Eriocaulon septangulare,* an *Odontoschisma elongatum-Cephalozia bicuspidata-Fossombronia foveolata* community or associule. This is described more fully under the Arenicolous communities (p. 286).

ground cover is now formed largely by mosses, with *Sphagnum* also becoming restricted in occurrence. Hepaticae now play a significant part only in the intermittently "raw" environments that become available, such as bark (*Frullania-Radula-Lejeunea* associule; occasionally *Ptilidium pulcherrimum* associule) and decorticated logs (facies of the *Nowellia-Jamesoniella* associule). On the ground, virtually no new Hepaticae come in, while the members of the *Mylia-Cladopodiella* associule drop out, one by one. This condition becomes more extreme, as the climax is attained, when the Hepaticae become totally restricted to bark and such secondarily "bare" environments as the xylem of fallen trees. The pH in the *Picea* forest will vary about that read at Kerrick (4.14 to 4.22).

PERENNIAL COMMUNITIES OVER LOOSE MINERAL SUBSTRATES

In this category we have a group of pioneer communities which undergo ecesis on moist sand, moist loam and clay, often on banks, and are pioneers under such conditions. These communities often disappear as soon as any perceptible amount of organic material accumulates (sometimes in consequence of their reaction on the microenvironment), in which case there is gradual succession towards the humicolous communities, and towards, eventually (in theory), the climax community. Furthermore, the present series of communities have in common the perennial character of its members: they have neither a compulsory dry resting period, nor a submerged period.

Regionally, communities of this type are relatively rare (at least in the coniferous zone); all of the members, locally, are essentially oxylophytic, or at least have a low lime tolerance.

COMMUNITIES OVER LOOSE, WELL-DRAINED, SANDY SOILS

Three associules occur regionally over such substrates, which are defined largely by their moisture requirements. These communities are either extremely rare locally, or (*Odontoschisma elongatum-Cephalozia bicuspidata* associule) may be nearly or quite lacking.

1. *Lophozia bicrenata* (*L. excisa*)—*Cephaloziella rubella* (*byssacea*) *Associule.*—This widespread community was first described by the writer for New York (1949), though Griggs (1935, 1937) described a somewhat similar community over N-free, very sterile volcanic soils, and Sharp (1939) noted the same community from Tennessee; recently also noted by McGregor (1955) for eastern Kansas. This community occurs in the coniferous zone largely over mineral soils near rock-outcrops, or even as a crevice-community; elsewhere, it is very widespread on acid sterile soils, in fields, sandy plains, etc. The regional rarity of this xeromorphic community is not quite explicable.

2. *Odontoschisma elongatum-Cephalozia bicuspidata Associule.* — This represents a sharply circumscribed community occurring always near acid lakes which have a surrounding sandy, wet "moor," on which locally we find *Sphagnum* undergoing ecesis. As a pioneer community under such conditions, we find the two type species listed above (occasionally with *C. bicuspidata* replaced by *C. ambigua*), associated with *Pellia epihylla, Fossombronia foveolata, Riccardia* (?*multifida*), occasionally *Calypogeia trichomanis* and *Scapania*

irrigua. Associated vascular plants are *Utricularia* sp., *Xyris* and *Eriophorum* and *Eriocaulon* spp., several orchids (notably *Pogonia ophioglossoides*), *Juncus* and *Carex.**

Intergrading (and perhaps successionally intermediate) between community 2 above, and the helophytic bog communities of acid moors, we find widely distributed in sandy areas (such as in the sandy Jack-pine Barrens of Northern Michigan, near Tahquamenon Falls, near Deer Park, etc.), an intermediate type of community:

3. *Lophozia capitata-Cladopodiella Facies, of the Mylia-Cladopodiella Associule* (see p. 285).—Over a thin, peaty layer, in boggy depressions of sand plains, usually under *Chamaedaphne calyculata*, we find a sandy-bog variation of the *Mylia-Cladopodiella* Associule. Under such sandy-moory conditions, *Lophozia capitata* (=*mildeana*) totally replaces *L. marchica*. Associated usually is *Cladopodiella fluitans*, more rarely *Gymnocolea inflata*. Occasionally *Cephalozia* and *Cephaloziella elachista* are associated. However, such species of *Sphagnum* moors as *Mylia anomala*, *Calypogeia sphagnicola*, appear to be quite lacking.†

This community, bearing evident close relationships to the *Mylia-Cladopodiella* community of *Sphagnum* bogs, may occur in moist depressions very close to the *Lophozia bicrenata-Cephaloziella* associule. I have noted the latter in the acid sand barrens, in low places, near Tahquamenon Falls, Michigan, under slightly more xeric conditions than the above community.

COMMUNITIES OVER LOAMY OR CLAYEY, POORLY DRAINED, WATER-RETAINING SOILS; USUALLY ON LOAM BANKS AND IN WET DITCHES

The present series of communities are related somewhat to those described from sandy, well-drained soils.‡ However, the present communities never show succession towards bog communities, but rather towards mesic humicolous communities. Again, this series of communities is poorly developed or rare in our coniferous forest region.

1. *Blasia-Fossombronia-Anthoceros Associule.*—Various local variations of this community are widespread, especially over moist clay, near springs, in wet ditches, under a wide variety of conditions which have in common a

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* This community appears to be more common in the mountains, where I have studied it at Zealand Pond (New Hampshire), and at Davis Pond, Mt. Katahdin, Maine. There we find the same group of species listed above, with, in addition, such more strictly subarctic-subalpine species as *Nardia geoscypha, Gymnocolea inflata, Cladopodiella francisci,* etc. The community bears direct relationships to the *Gymnocolea-Cephalozia bicuspidata* pioneer community of dripping talus and waterfalls, and of sunny, acid rock-pools (see p. 263). Locally, this associule has been found only at Deer Lake, Baraga County, Michigan, west of Pictured Rocks.

† A *Lophozia capitata-Fossombronia foveolata-Cephaloziella rubella sullivantii-Pellia epiphylla* community of the boggy *Chamaedaphne* meadow, at Ham Lake, Minnesota, on the Anoka Sand Plain, appears to represent an attenuated and degraded phase of this community; it has not been noted elsewhere in Minnesota. (See also under p. 285.)

‡ Indeed, the *Lophozia bicrenata-Cephaloziella rubella* associule occurs indiscriminately as a pioneer associule over either sandy soils, or acid loamy soils, or calcareous loamy soils (then often consociated with *Solenostoma crenulata, Lophocolea minor* in a *Lophozia-Cephaloziella-Solenostoma* facies); this does not appear to occur anywhere regionally in the coniferous region).

fairly sunny, quite moist to wet, environmental complex of factors. Several facies may be distinguished.

A. BLASIA FACIES: Over moist clayey banks (as on Bark Point, Wisconsin; over springy clay bank at Lake Superior shore, Porcupine Mts., Mich.; S. of Duluth, Minn.) we may find a *Blasia* consociation, often with *Marchantia polymorpha* mixed in (as at the Porcupine Mts.). Rarely associated is *Fossombronia foveolata*, occasionally *Anthoceros* in small quantities, occasionally (but apparently never locally) *Solenostoma crenulatum*. This community occurs equally well-developed in the deciduous forests (see p. 296).

B. MARCHANTIA FACIES: Over moist clayey soils, *M. polymorpha* often forms large, almost closed stands (as on springy, clayey soil near bog in N. edge Anoka County, Minn.).

C. RICCARDIA PINGUIS-MOERCKIA HIBERNICA FACIES: Over evidently calcareous clay banks, and ditches, may occur a consociation of *R. pinguis*, *M. hibernica*, at times with *Preissia quadrata* and *Marchantia* (well-developed at Angle Inlet, Minn., west of the "town" in loamy-clayey ditch along road). A *Riccardia-Marchantia* variation common under *Equisetum variegatum* and *E. hyemale* occurs at a springy, clay slope near Munising, Mich.; this and forms intergrading to it are also described by the writer (Schuster, 1949) as the *Riccardia-Moerckia* facies, for central New York.

D. PELLIA-FOSSOMBRONIA-ANTHOCEROS FACIES: Rare or absent in the coniferous region proper, though in the borderline area at St. Croix State Park, this community occurs (see p. 296). First described (by Schuster, 1949) for central New York as a discrete associule; however, it grades so completely into the above community (delimited by a tolerance or dependence on lime) that it can be separatd only because it is widespread in lime-free regions (though it also tolerates lime). pH 5-5.8 (at St. Croix), rarely higher.

XEROGEOPHYTIC AND HYDROGEOPHYTIC COMMUNITIES

In dry, sunny areas where a summer aestival period occurs, as well as in open, sunny fields, where a winter period of submersion may exist, we find communities of annual plants with large spores. These communities are always pioneers of moist, sandy (more rarely clayey or loamy) soils, more rarely over soils over dry rocks. They share in common with the arenicolous communities (treated immediately above) a certain number of species, among them chiefly species of *Anthoceros* and *Riccia*.

Communities of this type are widespread in climates with hot, dry summers, but are rare in the coniferous region; they appear to be quite absent from the coniferous region in our area, but are poorly represented in the deciduous forest region, and better developed in the prairie (see pp. 297-98).

PLANKTONIC COMMUNITIES (Errantia)

A pair of communities occur, common to both the coniferous area and deciduous area. These communities are treated under the deciduous forest region (see p. 298), since they are much more common there. At least one of them (The *Ricciocarpus-Lemna-Wolffia associule*) appears to occur, even though rarely, into the northern edge of the boreal coniferous forest climax region, (fide Steere, 1951).

COMMUNITIES OF THE DECIDUOUS FOREST FORMATION

A variably wide strip running approximately from SE to NW, is covered by various manifestations of deciduous forest; this borders the coniferous

forest formation, treated previously. This strip may be very narrow in the NW region, where prairie and coniferous forest may actually be locally contiguous (see fig. 23), but is particularly well-developed in the southeastern corner of Minnesota.* For this, and other reasons, the following discussion is based largely on the deciduous forest as it occurs in the eastern one-third of the state; elsewhere it has been studied only in the Minnesota River valley, near Grand Rapids.

For our purposes, this deciduous forest may be divided into three basic manifestations, a) the basswood-maple forest (climax), which is generally agreed to represent a somewhat more xeric, western, attenuated form of the more easterly beech-maple climax; b) the elm-red maple-willow-cottonwood bottom forest (generally considered to be disclimax) fringing the Mississippi, Minnesota and St. Croix rivers, extending for a variable distance up the rivers into the prairie (where it is postclimax); c) the more xeric oak-hickory or oak forests, sometimes called the oak-savannah, which form an ecotone between the basswood-maple and the prairie climaxes. Hepaticae are almost absent in the latter forest type, except in small ponds (*Riccia* and *Ricciocarpus* communities); so this will not be treated here. The associules of the other two forest types, in which Hepaticae play a part, tend to be much the same except that, naturally, the loam and clay-bank associules of river-banks are to be expected more commonly in the elm-red maple-willow-cottonwood forests.

EPIPETRIC COMMUNITIES

The epipetric communities of the deciduous forest are extremely poorly developed, and very local in Minnesota and the surrounding area. Partly responsible is the attenuation of the epipetric flora, associated with the relatively unfavorable P/E ratio, the relatively low (28-32 in. or less) rainfall, and the limited types of rock outcrops. Indeed, communities in which Hepaticae play any considerable part are rare, even more so than communities in which mosses play an important part. The following treatment reflects the attenuated version of the epipetric community-complex which occurs regionally. It should be pointed out that each of the communities briefly dealt with recurs in much more luxuriant and polytypic versions in the deciduous forests of the Appalachians, particularly of the southern Appalachians, where the epipetric communities are as complex and difficult to deal with as are the epipetric communities of the regional coniferous forest. Indeed, the local epipetric communities found in the deciduous forest biome represent in all but a few instances mere vestiges of more complex and much richer communities of the area to our east. The Tertiary relicts and endemics which characterize many of these communities in the Appalachians (such as *Plagiochila austinii*, *P. caduciloba*, *P. virginica*, *P. sullivantii*, *Acrobolbus rhizophyllus*, *Metzgeria hamata*, *Solenostoma obscurum*, etc.) are wholly unknown from our immediate

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* As will be noted, the deciduous forest of the SE. corner of the state receives 32 in. of rainfall annually; it is, in fact, the only area within the deciduous forests of Minnesota where rainfall (and the P/E ratio) is adequate enough to support other than extremely attenuated forms of the bryophytic communities, such as described, for instance, in Schuster (1949, pp. 143-159).

nity is much attenuated, compared with its high development in the boreal coniferous forest region, and based on Ca tolerances, can be subdivided into two groups.

A. CALCIPHILE LOPHOZIA (LEIOCOLEA) BADENSIS (MUELLERI) COMMUNITY: This was described by the writer (1949, p. 662) from similar sandstones and lime-stones in New York. Locally, we find outcrops of *Gymnostomum* and other "calciphilous" mosses, associated with *Lophozia badensis*, often with *Riccardia pinguis* (as at Crystal Springs, Wisconsin). At other times, *L. muelleri* fo. *pumilla*, which is very close and deceptively similar to *L. badensis*, replaces the *L. badensis*; we may still then find *Riccardia pinguis* consociated (as at Wabasha and at the Sugarloaf, Winona). As there is accumula-tion of soil, succession occurs towards the *Preissia-Mannia-Reboulia* community (p. 292).

B. CALCIPHOBE LOPHOZIA-SCAPANIA COMMUNITY: This is extremely poorly known from the sandstones of the Mississippi Valley; Conard describes a community of *Scapania nemorosa-Tritomaria exsecta* and *T. exsectiformis* from NE. Iowa, that represents an attenuated version of the *Lophozia alpestris-Scapania nemorosa* community. On Gwynn's Bluff, we find *Scapania mucronata* over acid sandstones. Near Winona, *Scapania nemo-rosa* occurs over sandstone. Over the sandstone at Taylors Falls is found perhaps the best-developed relict of this northern community, consisting of *Scapania mucronata* and *saxicola*, *Tritomaria exsectiformis*, *Lepidozia reptans*, *Solenostoma hyalinum* and *S. fos-sombronioides.** An attenuated version also occurs on the sandstone along the Mississippi River in Minneapolis, where *Lophozia excisa* and *Scapania mucronata* occur together.

All of the community-fragments of this type, locally, appear to represent attenuated relicts of the *Lophozia-Scapania* associule of the coniferous region.

3. *Ptilidium pulcherrimum Community.*—Over dry sandstones, as at Wi-nona, occurs a pioneer community formed by *Ptilidium pulcherrimum*. This, zonationally, intergrades with the following somewhat more mesic community on the same rocks.

4. *Jungermannia lanceolata-Jamesoniella Community.*—Over shaded, rather moist sandstone, as at Winona, and (without the *Jamesoniella*, but with *Scapania mucronata*, intergrading to the *Lophozia-Scapania* associule) at Tay-lors Falls, as well as near Whitewater State Park, etc., occurs this rare and scattered community, usually not strictly pioneer, since formation of a thin soil layer often precedes its ecesis. (This same community, together with *Solenostoma sphaerocarpum* and *S. levieri*, etc., occurs on Sand I., Wisconsin. This community occurs on moist, very shaded vertical sandstone walls; it is evidently a relict community, much as is the similar *Lophozia-Scapania* associule).

At Taylors Falls occurs an allied community, limited to rocks along brooks, which is distinct enough to warrant its separate mention.

5. *Solenostoma hyalinum-S. fossombronioides-Chiloscyphus pallescens-Pellia epiphylla Community.*—Found over sandstone blocks and ledges, often with *Phaeoceros laevis* (rarely with a little *Scapania saxicola* locally), this community (dominated by entire-leaved Jungermanniaceae) occurs under shaded, moist conditions with the pH locally from 7.0-7.3. It appears confined to rocks and ledges which are subject to periodic (if rare) submersion during

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* A similar community occurs over the basalts on the Wisconsin side of the St. Croix River, much more typical of the coniferous region, consisting of *Scapania nemorosa* and *S. mucronata*, *Lophozia incisa*, and *L. barbata*, *Tritomaria quinquedentata*. However, even this community is much attenuated, and evidently relict in nature.

flood periods. The community is much better developed eastward, especially in the Piedmont of Virginia to South Carolina, along streams, on rocks subject to inundation. In addition to the above species, *Conocephalum conicum*, rarely *Marchantia polymorpha*, occasionally *Solenostoma pumilum* and *S. crenuliformis* are associated. Eastward the community often occurs under weakly acid conditions.

B. *Communities of thallose (rarely leafy) types, usually, but not always undergoing ecesis subsequent to the deposition of small amounts of soil; often occurring long subsequent to soil-deposition and then scarcely epipetric. These communities are locally distinctly calciphilous, or at least "tolerant."*

1. *The Xeric Reboulia Associule.*—Usually under very exposed, sunny situations, *Reboulia hemisphaerica* is the only species of hepatic undergoing ecesis on rocks, or thin soil over rocks. Under mesic extremes (as at Taylors Falls), *Phaeoceros laevis* and *Solenostoma hyalinum* may occur with it, at which point it intergrades to the preceding community.

2. *The more Mesic Preissia-Mannia rupestris-M. sibirica Associule.*—Very closely related to the above community, but undergoing ecesis more usually in somewhat shaded or on somewhat damper rock-walls. In addition to *Preissia quadrata*, the thallose *Phaeoceros laevis* often undergoes ecesis under such conditions.

A. PREISSIA-PHAEOCEROS LAEVIS COMMUNITY: This community occurs commonly on rather exposed vertical sandstone walls as near Winona, Minn.

B. PREISSIA-MANNIA RUPESTRIS COMMUNITY: This community occurs near Stillwater in Whitewater State Park and elsewhere in SE. Minnesota, as well as in NE. Iowa. Under somewhat more xeric conditions, we find the following facies:

C. PREISSIA-MANNIA-REBOULIA COMMUNITY: Under generally more sunny, less constantly damp conditions, *Preissia* is accompanied on nearly bare rocks by *Mannia sibirica* and occasionally *Reboulia hemisphaerica*.

3. *Clevea-Mannia Associule.*—Over the crests of cliffs, on thin soil (especially on narrow ledges, and on thin soil over steep, partly exposed talus), the arctic-alpine *Clevea hyalina* occurs in scattered localities in SE. Minnesota from Wacouta to the Iowa border. Associated very commonly with it, under many conditions, is *Reboulia hemisphaerica*, a paradoxical combination of a temperate-zone indicator species, with an essentially arctic-alpine one. More commonly we find the arctic-alpine *Mannia sibirica* associated, in the following facies:

A. CLEVEA-MANNIA SIBIRICA COMMUNITY: Occurring widespread over shaded and relatively cool ledges in SE. Minnesota, always on the crests of E. or NW. facing bluffs, above the Mississippi River.
Nearer the crests of the ledges, occurs a more exposed, more thermophile facies.

B. CLEVEA-MANNIA FRAGRANS COMMUNITY: This xerothermophile community has been widely studied in Europe, but never reported from the New World. Locally it occurs at Wacouta and undoubtedly elsewhere.

C. *Communities of leafy species, usually undergoing ecesis after some preparation by mosses; found locally only over basic or circumneutral sandstone.*

*Including two communities locally, the first of which intergrades freely
with both the Reboulia and the Preissia-Phaeoceros communities.*

1. *Lophocolea minor-Chiloscyphus Community.*—Occurring usually on
moist shaded rock-walls (occasionally with *Scapania mucronata* and *Lophozia
excisa* and *Cephaloziella hampeana* as at Minneapolis; then grading into the
Lophozia-Scapania associule). Both *Lophocolea minor* and *Chiloscyphus pal-
lescens* facies of this community occur, but need not be treated separately here,
since they are so rare in occurrence.

At Whitewater State Park over basic soil and on sandstone talus, a *Lopho-
colea minor-Jungermannia lanceolata* facies occurs, intergrading evidently
with the *Jungermannia-Jamesoniella* community cited previously.

2. *Plagiochila asplenioides Community.*—Closely related in physical re-
quirements to the preceding but usually undergoing ecesis only after consider-
able soil has accumulated, and in dense shade. Locally rare, but occurring, for
instance, with mosses at Lake City. In the Appalachian system a widespread
community, associated, on soil-covered rocks or clay to loam banks, with a
variety of other species (often *Scapania nemorosa*, occasionally *Pellia epiphylla*,
etc.).

EPIPHLOEMIC AND EPIXYLIC COMMUNITIES

The communities undergoing ecesis on bark of trees, and on logs, are
developed to a much poorer degree in the deciduous forest than in the conifer-
ous forests. The reason lies to a very large degree in the fact that a larger
number of species occur on such habitats in the coniferous forests, therefore,
the communities are more complex. However, the much less favorable P/E
ratio in the deciduous forests undoubtedly plays a very important role in
strongly restricting the occurrence of these communities in the basswood-
maple forests. The following analysis of the communities is thus much
simpler than the similar analysis given by the writer for the deciduous forests
of central and western New York (1949). The attenuated form of the
communities is, in part at least, due to the fact that as the deciduous forest
becomes more open, as one approaches the prairie, increased insolation becomes
an effective factor in limiting the ecesis of many species. However, many
species (such as *Metzgeria furcata, Lejeunea ulicina*) simply do not occur this
far from the Appalachian regions that represent the center of their post-
Pleistocene dispersal.

EPIPHLOEMIC COMMUNITIES

The corticolous associules of the deciduous forests, like those of the
coniferous forests, are relatively simple locally—those in which Hepaticae
play an important role all belong to various manifestations of the following
associule.

1. *Frullania-Radula-Lejeunea Associule.*—The manifestations of this asso-
ciule differ from those of the coniferous forests chiefly in that *Radula* is almost
consistently absent—largely because of the inability of the local species of that
genus to tolerate a high saturation deficit. The following local facies occur,
some very rarely; they are often nearly identical with the facies occurring nearby
on rock-outcrops.

A. FRULLANIA RIPARIA FACIES: Occurring rarely, and then usually over the bark of climax forest trees, such as *Tilia* on forests of talus slopes adjacent to cliffs; the species much commoner on cliffs and populations on these undoubtedly serve as a reservoir from which the occasional epiphloemic manifestations are derived. Frequent in Whitewater State Park, Winona Co.

B. FRULLANIA EBORACENSIS-BRITTONIAE FACIES: Very widespread on a variety of trees—*Tilia*, *Quercus*, *Fraxinus*, *Acer*, etc. Under some conditions, particularly along flood-plain forests, or those adjacent to shaded bluffs, we occasionally have *F. inflata*, replacing the more xeromorphic *F. eboracensis*. *F. bolanderi* also occasionally replaces these species in the areas adjacent to the "Driftless" region, and to its north. It is occasional both on *Quercus alba*, on the exfoliating bark of *Betula cordifolia*, as well as on *Tilia*.

C. PORELLA PLATYPHYLLOIDEA FACIES: Very occasionally on bark of a variety of trees, in areas with a relatively low saturation deficit (especially near streams), *Porella platyphylloidea* (or, more rarely, *platyphylla*) replaces the above species of *Frullania*.

D. COLOLEJEUNEA BIDDLECOMIAE FACIES: Extremely rare in the deciduous forest region, and reported only by Conard from our area. Found once in Allamakee Co., Iowa, on the twigs of the shrub *Taxus canadensis*—which grows in that area only on shaded, moist cliffs, where the saturation deficit is unusually low for the region as a whole.

As we approach the ecotone area between deciduous forest and coniferous forest, as in the Cedar Creek Bog area, Anoka Co., Minnesota, we begin to find the *Radula-Frullania* facies, chiefly *Radula complanata* and *Frullania eboracensis* and *F. bolanderi*, usually on the bark of *Thuja*. This occurs rarely or not at all in the strictly deciduous forests regionally. As we go eastward into Wisconsin and Michigan, it descends southward into the deciduous forest, since the P/E ratio becomes less suboptimal as we go eastward.

EPIXYLIC COMMUNITIES

These communities are equally attenuated in the deciduous forests regionally. In the relatively xeric basswood-maple forests they virtually have no opportunity to develop, and it is only as we go eastward into Wisconsin and Michigan, where they begin to achieve a complexity and frequency such as was described by Schuster (1949) for the deciduous forests of central and western New York. Two associules are represented locally.

1. *Nowellia-Jamesoniella Associule.*—Neither of the two type members of this Associule appear to occur, except as extreme rarities, on logs locally. The community occurs in a locally rare manifestation.

PTILIDIUM PULCHERRIMUM FACIES: Found once or twice, as in Beaver Valley State Park (Houston Co., Minn.) but so rare as to be ecologically insignificant locally. No other species of Hepaticae associated, but pleurocarpous mosses frequent.

2. *Bazzania-Blepharostoma-Lepidozia Associule.*—Occurring on moist, much disintegrated wood (and successively following the *Nowellia-Jamesoniella* associule). In the coniferous forests this community is widespread (p. 278), but in the deciduous forests only remnants exist locally, usually quite devoid of the *Blepharostoma* and *Lepidozia* (which become rare and restricted to shaded moist sandstone rock bluffs). Two local facies are present.

A. MESIC TETRAPHIS-BAZZANIA-CEPHALOZIA MEDIA FACIES: Over moist, but not wet decayed stumps and logs (as in Anoka County); peripheral in distribution, but becoming commoner in the more mesic forests eastward, where the community extends much further southward in the Appalachians. Occasionally *Lophocolea heterophylla* is consociated.

B. HYGRIC CALYPOGEIA MEYLANII-GEOCALYX GRAVEOLANS-LOPHOZIA INCISA FACIES: An attenuated version of the similar facies of the coniferous forest region, differing in the absence of *Tritomaria* (which becomes rare and restricted to rock-walls southward). Occurring locally as far south as Taylors Falls (on decayed moist stumps on the

moist shaded bluffs on the Wisconsin side of the St. Croix River), but extending much
further south as one goes eastward. Because of the less mesic forests of the region, this
community is much more poorly developed than in the beech-maple forests eastward.

C. HYGRIC CONOCEPHALUM FACIES: Occasionally over wet, much disintegrated
logs, especially near stream or small brooks. *Conocephalum* may form large patches,
sometimes with *Mnium* and other mosses of mesic-hygric sites. Locally scarce, but found
(for instance) near the Minnesota R., west of Minneapolis.

It should be emphasized that much more detailed study of the epixylic
communities in the deciduous forest region just south of the coniferous forest
border will undoubtedly show more complex facies of the above communities;
however, in most cases these will prove to be associated with bog forests, where
there is clear intergradation to the communities treated under this heading,
for the coniferous forest (p. 276).

HUMICOLOUS COMMUNITIES

Occurring over the ground, away from rock-outcrops, and not on decaying
logs, in subclimax and climax forests, are a very limited series of bryophyte
communities. In the climax basswood-maple forest, Hepaticae are either
totally or virtually absent, even though moisture conditions are adequate
enough. The reason for this appears to be the dense annual accumulation of
forest litter as pointed out by Schuster (1949) for the similar beech-maple
forest to the east. On the other hand, in the subclimax forests, conditions
regionally are generally much too xeric for the ecesis of other than a very
few hardy and ubiquitous Hepaticae. The following are the only species that
I have seen over moist humus, and away from rocks and logs locally: *Lopho-
colea heterophylla; Lophocolea minor* (usually not far away from basic
rock-outcrops); *Conocephalum conicum* (usually near brooks or other sources
of water); *Bazzania trilobata* (rare; of peripheral occurrence). In no case can
we speak of the Hepaticae as abundant enough under humicolous conditions
that distinct associules are involved.

HELOPHYTIC COMMUNITIES

Because of the relatively low rainfall (32 in. or less), the deciduous forest
region is nearly free from swamps (except along rivers) and quite free from
bogs. Helophytic communities are therefore only of sporadic occurrence until
the ecotone area north of Minneapolis is passed, where we get islands of boreal
bog forest (as in Anoka Co.). Such ecotone areas usually show a much
poorer, attenuated version of the helophytic successions than we get in the
boreal forests. A very few examples are at hand that show us the hepatic
constituents of these areas.

In a marly-peaty meadow near Savage, Dakota County, occurred *Riccardia pinguis*
(part of an attenuated marl-bog sere).

At Cedar Bog, Anoka Co. (actually in the ecotone from Deciduous to Coniferous
Forest) the marly lake is surrounded by a sedge mat with very sparse *Riccardia pinguis*
in it, and some *Marchantia;* in moist, less marly situations more peripheral to the marl
pond occur large quantities of *Marchantia,* but no *Riccardia.* Near the periphery of the
bog, a poor *Chamaedaphne* heath (with *Ledum* and *Vaccinium oxycoccos,* but not *Chamae-
daphne*) stage occurs, with traces of the acid-bog stages on logs and among *Sphagnum*
(*Cephaloziella elachista* traces; *Cephalozia media,* C. *pleniceps,* and C. *connivens, Odonto-
schisma denudatum, Calypogeia meylanii* on logs, etc.).

Though these traces occur in the ecotone area between coniferous and deciduous forest,
it is almost no exaggeration to state that the helophytic communities are virtually absent

in our region in the deciduous forest zone. Careful study near Lake Itasca reveals the same basic distribution of species as at Cedar Bog: an attenuated marl-bog sere, associated with the presence of *Thuja* and black spruce, in an ecotone area between deciduous and coniferous forest.

PERENNIAL COMMUNITIES OVER LOOSE, MINERAL SUBSTRATES

This series of communities include species able to undergo ecesis on mineral soils and sands; furthermore, they almost all seem to disappear as a considerable humus layer is developed. Regionally, two basic communities of this type occur.

1. *The Xerothermophyte Mannia fragrans Associule.*—Occurring over sunny, exposed sandy terraces along rivers (as at the St. Croix and Minnesota Rivers), usually actually in prairie microenvironments. (See under the Prairie Communities).

2. *The Fossombronia-Blasia-Anthoceros Associule.*—In contradistinction to the above community, this occurs in forests only over soils of a finer consistency (usually sandy loam or clay). The community is particularly well-developed some 8 mi. S. of Winona, where we find it in abundance along an intermittent rivulet, cutting through a clay-loam bank. Associated are *Blasia pusilla* with *Phaeoceros laevis, Conocephalum conicum,* and *Riccardia pinguis,* occasionally *Chiloscyphus pallescens. Fossombronia* has not been found and appears to be quite lacking from the few associules of this type that have been found in Minnesota. The community at Winona may be separated into two facies.

A. BLASIA-ANTHOCEROS FACIES: With *Riccardia pinguis* as an accompanying species.

B. PELLIA-ANTHOCEROS-FOSSOMBRONIA FACIES: Along the banks of the St. Croix River at St. Croix State Park occurs a better developed facies, present on springy banks, characterized by the presence of *Pellia epiphylla* and *P. neesiana, Phaeoceros laevis* and *Anthoceros macounii,* and *Fossombronia foveolata. Conocephalum conicum, Marchantia* and a very little *Blasia pusilla* are the accessory species. The pH at this site was 5.0-5.8.

The two preceding faciations could perhaps be classed with the xerogeophytic communities, since they are characterized by large-spored species, which either die back very much (*Blasia*) or are nearly or quite annual locally (*Anthoceros, Fossombronia*). However, the common occurrence of purely perennial types (*Pellia, Conocephalum, Riccardia pinguis*) associated with these species, together with the absence of strongly intermittent moisture conditions during the summer growing season, suggest that the community is sociologically more closely allied to the other arenicolous communities. Furthermore, elsewhere we find close intergradation to the following clearly perennial community.

3. *Solenostoma crenulatum-Scapania nemorosa Associule.*—This associule is an extraordinarily common one southward in the Mississippi Valley, forming one of the commonest bank communities in which Hepaticae take place in areas such as noncoastal Mississippi and Louisiana, north to Missouri and Connecticut (there often grading into the *Lophozia bicrenata-Cephaloziella* associule, which is restricted locally to the coniferous forest). Often associated are *Calypogeia fissa* and *C. muelleriana,* occasionally *Cephaloziella rubella* in

drier areas (then grading into the *Lophozia bicrenata-Cephaloziella* associule).
Regionally, only attenuated forms of this community occur, the *S. crenulatum*
having been collected a single time in Iowa and Minnesota each, but becoming
much commoner eastward and southward.

On moister banks, this community also may intergrade with facies of the
Fossombronia-Blasia-Anthoceros associule (as noted in Schuster, 1949, p. 148).
Southward in more austral regions, *Odontoschisma prostratum* becomes a
commonly associated member, as well as (in sunny sites) *Asterella tenella*.

XEROGEOPHYTIC AND HYDROGEOPHYTIC COMMUNITIES

Including communities of southern affinity whose members have a distinct,
obligatory annual resting stage usually in the spore stage. Included are essen-
tially the *Riccia* Communities, associated with which we often find *Anthoceros*
and *Notothylas* (genera which are normally annual locally). Several possible
facies occur, all members of the following basic associule.

1. *Riccia-Ricciocarpus-Anthoceros Associule.*—Occurring usually on soils
that are much disturbed either in fields or along paths near streams. A single
local, rare facies occurs.

RICCIA FROSTII-R. CRYSTALLINA-RICCIOCARPUS FACIES: Occurring over relatively
moist, shaded, compact mineral soil, as at Minneapolis. Usually limited to areas near
water, often on alluvial soils only, since the spores are water-disseminated. The common
presence of *Ricciocarpus* (a member of the following associule) is indicative of the mesic
habitat these species frequent.*

The above communities, in many cases, freely intergrade with the *Fossombronia-Blasia-
Anthoceros* associule, treated immediately previously.

2. *Riccia beyrichiana-sorocarpa-hirta-austinii Associule.* — Occurring much
further from water in drier sites where summer aestivation must occur. This
community has been found a single time in Minnesota along the Minnesota
River, associated with the disjunct *Riccia trichocarpa.*

The two preceding communities are only superficially allied. The *Riccia
frostii-crystallina-Ricciocarpus* Community is essentially hydrogeophytic and
dependent on water dispersal of its spores; it does not have a summer aestival
period, and the species mature their spores in autumn. The community, as
has also been recognized by McGregor (1955), is essentially restricted to
alluvial soils, or at least to areas subject to flooding.

In contrast, the *Riccia-beyrichiana-sorocarpa-hirta-austinii* associule is essen-
tially an xerophytic community, almost wholly restricted to soils not subject
to inundation.† The community is one of temporary habitats (such as

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* It is significant that along the Mississippi River at Minneapolis, *R. frostii* and *R.
crystallina* occur consociated with *Ricciocarpus;* again, over 900 miles to the south along
the Mississippi River near Rosedale, Mississippi, this same association of *R. frostii* and
Ricciocarpus is common.

† The members of this community vary widely as to the time at which spores are
produced. In the south they are often somewhat biennial, often grow chiefly from early
fall to early spring, producing their spores from October or November through March,
rarely as late as April. In our area, the members of this community are apparently largely
or wholly annual, developing from spores in the spring until September, when spores are
produced. Southward, therefore, this community has an aestival period, or summer rest
period; northward such a period seems to be lacking.

fallow, exposed fields), varying widely in degree of development. Often associated are various pigmy mosses (*Physcomitrium, Nanomitrium, Ephemerum, Pleuridium,* etc.), and more rarely *Anthoceros crispulus.* This community is much more widely developed southward, even though it may include, regionally, such southern types as *Riccia trichocarpa* and *R. dictyospora.* However, such index species of the Lower Austral zone as *Sphaerocarpus texanus* are wholly lacking locally.

PLANKTONIC COMMUNITIES (Errantia)

Of very limited distribution in the state, occur a pair of associules including both Hepaticae and reduced angiosperms. This pair of associules occurs most commonly in and adjacent to deciduous forest regions, more rarely in the coniferous forest (see p. 288), but also in ponds and slow streams in the prairie.

1. *Floating Ricciocarpus-Lemna minor-Wolffia Associule.*—Consisting of the hepatic *Ricciocarpus natans* and the duckweeds *Lemna minor* (occasionally *Spirodella polyrhiza*), and *Wolffia columbiana;* common as a pioneer community in shallow waters. As the water dries out during the summer in shallow ponds, especially in the Prairie, this community occurs stranded on soil, together with members of the next associule.

2. *The Riccia fluitans-Lemna triscula-Utricularia Associule.*—Consisting of the common *R. fluitans,* with narrow thallus segments (the apparently much rarer *R. rhenana* has not yet been found locally), associated with *Utricularia vulgaris,* etc., and *Lemna trisulca.* Characterized by the fact that a different stratum is inhabited than by the associule treated immediately above, the plants usually growing in the ½-2 in. zone immediately beneath the water surface.

COMMUNITIES OF THE PRAIRIE FORMATION

By the very nature of the microenvironment that results in a prairie vegetation, we would not expect to find any extensive development of Hepaticae. In almost every case, Hepaticae are limited to, or adjacent to, the narrow strips of Postclimax Forest that penetrate the prairie along rivers and streams. Only two associules regularly occur in or adjacent to the Prairie.

1. *Mannia fragrans Associule.*—Occurring often over sand terraces, inhabited by prairie vegetation (*Geum triflorum, Anemone patens* var. *wolfgangiana, Lithospermum canescens* and *L. croceum, Viola pedatifida* and *V. pedata,* etc.) as well as the usual prairie grasses, such as *Bouteloua* and *Andropogon.* Here we find large growths of *Mannia fragrans* occurring in open areas, between tufts of grass, associated with such weedy mosses as *Bryum argenteum,* but with no other Hepaticae. In other cases, the same vascular flora (and same mosses and hepatics) occur consociated on the exposed crests of the Mississippi River bluffs ("Goat Prairie") and in Whitewater State Park. In almost all cases, the *Mannia* is a clear index species of prairie conditions, adjacent to the deciduous forest. However, the species appears to be lacking totally when the main body of the prairie is reached. For instance, it is common near the postclimax river forests in western Minnesota, at Grand

Rapids, but is not known elsewhere from the strict prairie regions of the western portions of the state.*

2. *Riccia beyrichiana-sorocarpa-hirta-austinii Associule.*—Found in semi-prairie habitats along the Minnesota River, not far from St. Peter. This associule of exposed soils is quite rare and appears to have been most often overlooked in Minnesota. *Riccia* communities will certainly prove more frequent, if looked for at the proper season (August-October) than they appear to be at present. It is not known how far this community will penetrate into the prairie proper, although phases of it are reported as common in the eastern half of Kansas (McGregor, 1955).

The two preceding communities represent the only ones definitely known from our prairie region. However, *Marchantia polymorpha* has been repeatedly seen along small prairie streams (particularly where these cut through rock, as in southwestern Minnesota).

It deserves emphasis that the *Riccia* associule, treated last, is not confined to the prairie: it recurs again in much of the deciduous forest region wherever temporary, raw substrates occur. For example, all of the species cited as typical of this community (*R. beyrichiana, sorocarpa, hirta, austinii*) occur in old corn fields near Durham, N. C., associated with *R. dictyospora* and other species. The various phases of the more or less xeromorphic *Riccia* associule, therefore, are to be classed as temporary elements in sites where pioneer conditions prevail. They undergo ecesis on broken soil, and are wholly unable to maintain themselves in areas where periodic disturbances does not occur.

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* It has been searched for carefully, without success, along the granite outcrops near Pipestone.

The Relation of Phytoplankton Periodicity to the Nature of the Physico-Chemical Environment with Special Reference to Phosphorus[1]

I. Morphometrical, Physical and Chemical Conditions

Allan Tucker

Michigan State University, East Lansing[2]

Inasmuch as phytoplankton is an important link in the food cycle for all living organisms in a body of water, knowledge of its abundance might well indicate the productive capacity of that body of water. In the past, the majority of investigations involving quantitative phytoplankton collections and analyses have been limited to summer months. The ineffectiveness of summer investigations in showing the true picture of phytoplankton production has been demonstrated by several workers, who conducted year-round investigations on various lakes in this and other countries. Among them, Dailey (1938) and Chandler (1940) have made such studies on Lake Michigan and Lake Erie respectively. Both have shown the occurrence of two large annual pulses, one in early spring and the other in late fall. Had these investigations been restricted to the summer months, the pulses in these lakes would never have been recorded. In seven small Colorado lakes which he studied the year-round, Pennak (1946) reported that

> Only one showed characteristic spring and autumn pulses. Another lake had three pulses, one in spring, one in mid-summer and one in autumn. Each of the other four lakes had only a single peak in the annual population curve; in three of these it occurred sometime during the spring, and in the other during the summer.

Because there may be one, two, three or no phytoplankton pulses in a lake annually, and since these may occur at any time of the year, it seems almost imperative to conduct year-round studies in order to gain a perspective of phytoplankton production.

Plankton samples and physical chemical data were collected from Douglas Lake for 16 consecutive months from July, 1950, through October, 1951. It is the main purpose of this paper to show the seasonal and vertical distribution of phytoplankton in Douglas Lake during that period of time and to discuss the possible roles of some of the physical chemical conditions—particularly phosphorus—in the metabolism of a lake. In addition, plankton samples and physical chemical data were collected during the summers of 1948, 1950 and 1951 from Munro, Vincent and Lancaster lakes in northern

Michigan and during the fall of 1950 from Lake Lansing in southern Michigan. These lakes are quite different morphometrically, and part of this paper will be devoted to a comparison of the phytoplankton and physical chemical conditions of those lakes during the periods mentioned.

Part I will deal with the morphometrical, physical and chemical conditions of the lakes investigated. Part II, consisting of a quantitative and qualitative analysis of the seasonal and vertical distribution of phytoplankton in these lakes and a discussion of the relation of phytoplankton periodicity to the environment, will be found on pp. 334-370.

Morphometry of the Lakes

Four of the lakes which were studied, namely, Douglas, Lancaster, Munro and Vincent, are situated in the northern part of the lower peninsula. All four lie in Munro township, Cheboygan County, and are only a very few miles from each other. Eggleton (1935) pointed out the fact that although these lakes are so near to each other, they differ markedly in their morphometric, physico-chemical and biological conditions. Lake Lansing, on the other hand, is about 240 miles south of the previously mentioned lakes. It is situated in Ingham County approximately three miles east of East Lansing.

The morphometry of the first four lakes has already been described in the literature and the following accounts mention only those salient features of each lake which are pertinent to the present investigation. References to the original descriptions are included.

DOUGLAS LAKE

The first hydrographic map of this body of water was made by the Department of Geodesy and Surveying of the University of Michigan, during the years when it maintained a surveying camp on the site where the University of Michigan Biological Station is now situated. Scott (1921) and Welch (1927) also thoroughly discussed the morphometry of this lake. It has an area of 5.83 square miles. Its maximum length is 3.8 miles and maximum width 2.27 miles. The maximum depth, standard low water datum, is 89 feet (27.1 meters). Welch (1927) discussed the seven distinct depressions within its basin and further pointed out that these depressions are isolated from each other by depth contours of 40 feet (12.2 meters) or less, and that from the standpoint of physico-chemical conditions, each depression behaves as a separate lake. The investigation discussed in this paper was carried out in the South Fishtail Depression which is situated in the southeast corner

of the lake. It has a maximum depth of 24 meters and is isolated from the other depressions of the lake slightly below the 9 meter contour. The area of the basin at that depth is 0.14 square mile.

LANCASTER LAKE

Eggleton (1935) prepared a hydrographic map of this lake and summarized its morphometric data in tabular form. It has a surface area of approximately 0.08 square mile (51 acres) with a maximum length of 0.4 mile and maximum breadth of 0.28 mile. The maximum depth which occurs near the center of the lake is 17 meters and the slope from surface to bottom is abrupt.

MUNRO LAKE

This lake was mapped by Welch and Eggleton in 1932; Welch (1938). It is a rather large and shallow bog lake having an area of approximately 0.8 square mile (512 acres), with a maximum depth of 4.2 meters. The major portion of the lake, however, has a depth not greater than 2 meters. The presence of a false bottom in this body of water makes it difficult to make a true sounding (Welch, 1938). The maximum length of the lake is 1.68 miles and its maximum width is 0.78 mile. As one would surmise from these data, the slope of its floor is gradual.

VINCENT LAKE

Morphometric information about this small bog lake is included in the unpublished thesis of Gorham (1931) and also in a paper by Welch (1938). Vincent Lake has a surface area of about 0.05 square mile (32 acres). Its maximum length and breadth are 0.3 mile and 0.22 mile respectively. It has a maximum depth of 6 meters, but as in Munro Lake, it also has a false bottom and hence accurate measurements of depth are difficult to determine. It has a gradual slope from surface to bottom, however, not quite as gradual as that in Munro Lake.

LAKE LANSING

A hydrographic map of Lake Lansing was made available to the writer by the Institute for Fisheries Research of the Michigan Conservation Department. From this map, various morphometric information was calculated. The area of the lake is 0.71 square mile (452.5 acres). Its maximum length is 1.26 miles whereas its maximum width measured at right angles to its long axis is 0.83 mile. Most of the lake has a depth of approximately 10 feet (3 meters). There are, however, two depressions; one in the northern part, the depth of which is 35 feet (10.7 meters) and which, incidentally, is also the maximum depth of the lake, and the other in the southern part, the depth there being 25 feet (7.6 meters).

General Procedure

During the summers of 1948 and 1950, the author established headquarters at the University of Michigan Biological Station and collected vertical series of quantitative net plankton samples for identification and enumeration from each of the four northern Michigan lakes, Douglas, Lancaster, Munro and Vincent. These collections were made with a Birge and Juday 10-liter

plankton trap, at about weekly intervals, from a single station in each of the four lakes. The stations chosen were located approximately in the center of each of the three smaller lakes and situated over the deepest part of the respective basins. The samples from Douglas Lake were taken from South Fishtail Bay. At the time of a plankton collection, a vertical temperature series was taken and a vertical series of water samples collected with a Kemmerer sampler for certain chemical determinations including dissolved oxygen, free carbon dioxide, carbonates, bicarbonates, pH, conductivity, and phosphorus.

The writer was fortunate in that Dr. William Pruitt, Jr., who spent the entire year in this region, consented to collect vertical series of plankton and water samples and to take temperatures from the Douglas Lake station during the fall, winter and spring of 1950-51. The samples were sent to the writer's permanent headquarters at Michigan State University in East Lansing where they were analysed. These analyses consisted of identification and enumeration of phytoplankton, and chemical analysis of the water samples for carbonates, bicarbonates and various fractions of phosphorus. In the summer of 1951, the writer returned to the University of Michigan Biological Station and continued the investigation on the four northern lakes, repeating the procedures of the summer of 1950.

The Lake Lansing investigation was carried on during the fall of 1950. Here the procedure was, in the main, the same as that in the northern lakes during the preceding summer. All the collections were made from a single station over the deepest part of the northern depression.

By way of summary, then, data were collected from each of the four northern lakes during the summers of 1948, 1950 and 1951. The data from South Fishtail Bay, however, were collected over a period of sixteen consecutive months from July, 1950, through October, 1951. Data from Lake Lansing were taken during the fall season of 1950.

Physical and Chemical Conditions

METHODS

Temperatures.—All temperatures except those from Lake Lansing were taken with an HB reversing thermometer. Those from Lake Lansing were taken with a Taylor maximum-minimum thermometer which had been calibrated against the HB reversing thermometer.

Conductivity.—Conductivity determinations do not appear in any of the tables; however, some determinations were made from water samples taken from the four northern lakes and will be mentioned in the discussion concerning the chemical results. These determinations were made with a Digby and Biggs Dionic Water Tester (Evershed, 1911). Conductivity is measured in reciprocal megohms.

Oxygen.—Dissolved oxygen was determined by the Rideal-Stewart modification of the Winkler method as given by *Standard Methods of Water Analyses.*

Free carbon dioxide, carbonates, bicarbonates.—All these were determined according to the procedures described in *Standard Methods of Water*

Analyses. For carbon dioxide determinations, N/44 KOH and phenol-phthalein were employed. Carbonates and bicarbonates were determined from phenolphthalein and methyl orange alkalinity titrations.

Hydrogen ion concentration.—This was determined in the field using color standard tubes and standard indicators prepared by the LaMotte Chemical Products Company.

Phosphorus.—Many investigators have postulated that phosphorus is a limiting factor in the production of phytoplankton in freshwater lakes. Such an hypothesis seems logical from a theoretical point of view when the following three facts are considered. First, phosphorus is an important element in the protein molecule. Second, it plays an important role in the energy metabolism of all living things. Third, it occurs in lakes but in very minute quantities. In order to test this hypothesis, extensive analyses of the various forms of phosphorus were made in addition to quantitative phytoplankton analyses.

Various methods have been used by different workers to determine the amount of inorganic phosphate phosphorus present in a sample of lake water. Most of them, however, are modifications of the colorimetric cerulemolybdate method described by Deniges (1920). The chemistry involved here can be explained very simply. When ammonium molybdate is added to a dilute phosphate solution, a colored phosphomolybdate is produced which, in turn, forms a blue, complex compound on the addition of a reducing agent such as stannous chloride. The different modifications of this method merely vary in the concentrations of the reagent solutions used, and the apparatus employed in determining variations in the color densities of the blue, complex compound. The method used in this investigation was modified from Ohle (1939) and is described in the following paragraphs.

Reagents

1. *Ammonium molybdate.*—10 percent ammonium molybdate solution, $(NH_4)_2 MoO_4$, was added to 50 percent sulphuric acid in the ratio of 1:3. This reagent was stored in an amber pyrex bottle and was made up fresh each week.

2. *Stannous chloride.*—1 g stannous chloride, $SnCl_2. 2H_2O$, was dissolved in 10 ml of 25 percent hydrochloric acid. Fresh reagent was made up every two or three days.

3. Phosphorus standard.—.0439 g of anhydrous potassium dihydrogen phosphate, KH_2PO_4, was dissolved in distilled water and made up to 1 liter. One ml of this solution contained 0.1 milligrams or 100 micrograms of phosphorus. The solution was diluted to the concentration of the desired standard. In this investigation the standard was made up to contain 10 micrograms per liter.

Apparatus

The instrument employed for measuring the densities of the blue color was an industrial model of the Klett Summerson photoelectric colorimeter with a red light filter No. 66 having an approximate spectral range of 640-700 millimicrons. The colorimeter is provided with solution cells of various sizes so that measurements can be carried out at different solution depths, depending on the color densities of the solutions. Most of the water samples analyzed in this investigation had very minute amounts of phosphorus so that all measurements were made using a solution depth of 40 mm. The scale reading is a measure

of the optical density of the colored solution as determined by the photo-electric cell. The optical density of the solution, according to Beer's Law, is theoretically proportional to the concentration of the colored substance. Therefore, the scale readings are directly proportional to the concentration of the substances being determined. A useful feature of this colorimeter is the logarithmically spaced scale divisions. This eliminates the necessity of preparing a calibration curve. Concentrations of solutions can be determined directly by calculations from the scale readings.

Procedure

1. 50 ml of lake water were measured into a 125 ml Erlenmeyer flask.

2. 0.5 ml of the molybdate reagent were added and the flask shaken until the solution was well mixed.

3. The mixture was then poured into the colorimeter solution cell, placed in the instrument, and a reading taken. This reading, if greater than zero, was attributed to any color originally in the water plus the color formed by the addition of the molybdate reagent. The machine is constructed in such a way that the pointer can be adjusted to zero for this reading.

4. The solution was poured back into the 125 ml Erlenmeyer flask and one drop of the stannous chloride reagent added. The solution was shaken and replaced in the colorimeter solution cell. The cell was inserted in the colorimeter and when the pointer had ceased to move, another reading was taken. The pointer ceased to fluctuate when the color had reached its maximum density, which occurred in about ten minutes. The difference between this reading and the reading in (3) was due to the blue color formed by the phosphorus upon the addition of stannous chloride. If the pointer had been adjusted to zero in (3), then, of course, the subtraction would not be necessary, and the final reading would be the desired result.

The same procedure was carried out with distilled water and the reading, which was usually about three Klett units, was attributed to the reagents themselves and hence three Klett units were subtracted from the results of any samples being analysed. Standard solutions of known phosphorus concentrations were treated in the same manner and in nearly every case it was found that two Klett units equalled one microgram of phosphorus. These figures might well vary in different machines.

The method just described is for the determination of the amount of inorganic phosphate phosphorus present in water. Determination of the amount of total phosphorus, including that phosphorus bound in organic compounds, necessitates first the breaking down of the organic phosphorus into inorganic phosphate phosphorus. The method used here for this process was modified from Robinson and Kemmerer (1930). Fifty ml of the water sample were measured into a 125 ml Erlenmeyer flask. To the water was added 0.1 ml concentrated sulphuric acid, 0.25 ml concentrated nitric acid, and 1.5 ml concentrated hydrochloric acid. The solution was heated on a hot plate over slow heat until thick, white fumes of sulphuric acid were liberated. When this occurred, there were usually only a few drops of clear liquid remaining at the bottom of the flask. If this liquid was not clear, the flask was heated for a few more seconds whereupon the liquid usually cleared. If, however, the remaining liquid did not become clear with this additional heating, 1.5 ml of concentrated hydrochloric acid and 0.25 ml of concentrated nitric acid were again added and the flask reheated until the sulphuric acid fumes were liberated once more. When the flask had cooled, 50 ml of distilled water were added and the flask shaken vigorously to distribute evenly the few drops of liquid which had remained at the bottom. The solution

was now analysed for inorganic phosphate phosphorus according to the method described previously, and the result was considered to be the total phosphorus present in the sample.

The different forms making up the total phosphorus in lakes have been classified according to two schemes. One scheme (Juday, Birge, Kemmerer and Robinson, 1928) divides the total phosphorus into two components, soluble inorganic phosphorus and organic phosphorus. The soluble inorganic phosphorus is in the form of inorganic phosphate phosphorus and is supposedly dissolved in the water, hence making it available to plant life. Part of the organic phosphorus is tied up in the organic compounds making up the protoplasm of the living organisms and part of it is in solution. Soluble inorganic phosphorus can be determined directly. The organic phosphorus is determined by first analyzing the water for total phosphorus and subtracting from this value the amount of soluble inorganic phosphorus. The difference is the organic phosphorus.

A second scheme which has been suggested by Ohle (1939) and Hutchinson (1941) divides the total phosphorus into suspended or sestonic phosphorus, and soluble phosphorus. The sestonic phosphorus may be subdivided into organic sestonic phosphorus and acid soluble sestonic phosphorus. The organic sestonic phosphorus includes organic phosphorus found in living organisms and in certain types of detritus. The acid soluble sestonic phosphorus is really inorganic phosphate phosphorus which has become adsorbed on molecules such as iron hydroxide. The soluble phosphorus is made up of soluble inorganic phosphate phosphorus and soluble organic phosphorus. The soluble organic phosphorus appears mostly in colloidal form; however, some of it may be adsorbed on particulate matter.

In order to determine the amounts of the different forms of phosphorus present in a sample of lake water, it is first necessary to determine the total phosphorus and the inorganic phosphate phosphorus in the sample. Part of the sample must be filtered through a very fine filter and the filtrate analyzed for total phosphorus and inorganic phosphate phosphorus. From the results of these analyses, the various forms of phosphorus can be calculated. The sestonic phosphorus is the difference between the total phosphorus of the unfiltered sample and the total phosphorus of the filtrate. The acid soluble sestonic phosphorus is the difference between inorganic phosphate phosphorus of the unfiltered sample and the inorganic phosphate phosphorus of the filtrate. If the acid soluble sestonic phosphorus is subtracted from the sestonic phosphorus, the difference is equal to the organic sestonic phosphorus. The soluble inorganic phosphorus is, of course, the inorganic phosphate phosphorus present in the filtrate. The soluble organic phosphorus is calculated by subtracting the inorganic phosphate phosphorus of the filtrate from the total phosphorus of the filtrate.

In the phosphorus analyses of the present investigation, a combination of schemes one and two were used. The total phosphorus in each sample was determined. The inorganic phosphate phosphorus was also determined and recorded as soluble inorganic phosphorus according to scheme one. Strictly speaking, not all of this inorganic phosphate phosphorus is soluble because some of it is in suspension as acid soluble sestonic phosphorus. However,

the amount of acid soluble sestonic phosphorus is usually so small that it is negligible. This form of phosphorus was determined only in a few samples from Lake Lansing. In the remaining samples it would be included in the soluble inorganic phosphorus and the sestonic phosphorus. The organic phosphorus was calculated according to scheme one whereas the sestonic phosphorus and the soluble organic phosphorus were determined according to scheme two. One point in connection with the filtration of the water sample deserves special comment. For this process Hutchinson (1941) used a 35-second membrane filter. In this investigation, a Seitz filter with three layers of Whatman's No. 44 filter paper was used. It was found that filter pads which are especially made for the Seitz filter could not be used, because quite often, the filtrate coming through one of these pads contained more phosphorus than the total phosphorus of the unfiltered sample. This would appear to indicate that the sample picked up phosphorus from the filter pad.

Length of time between collection and analyses.—All of the water samples were analyzed within six hours after collection, except those that were collected at the Douglas Lake Station from September, 1950, through May, 1951. These had to be shipped by express from Cheboygan to East Lansing, and hence were three days on the way. A few drops of chloroform were added to each sample at the time of collection. The samples were analyzed for phosphorus, carbonates and bicarbonates immediately upon their arrival at the laboratory in East Lansing. Other determinations, such as dissolved oxygen, free carbon dioxide and pH could not be done on these samples, inasmuch as such determinations must be made very soon after the collection of samples.

DATA

DOUGLAS LAKE

Several papers have been written which include tables or discussions pertaining to the physico-chemical conditions in South Fishtail Bay. Most of them are restricted to the summer seasons (Welch, 1927; Eggleton, 1931; Welch and Eggleton, 1932, 1935). One series of such data, however, was collected from this station by Miller (1936) for twelve consecutive months between September, 1933, and August, 1934.

All the data included in table 3 were collected by the writer through sixteen consecutive months between July, 1950, and October, 1951, except certain of those for oxygen, carbon dioxide and pH. As has been explained previously, the water samples collected from Douglas Lake between September 16, 1950, and June 21, 1951, had to be sent to the writer in East Lansing for analysis, and hence were *en route* about three days. Determinations for these particular chemical conditions must be done either at the time of collection or shortly thereafter, and if determinations had been made on these samples, they would not have given the true picture of oxygen, carbon dioxide and pH values in the lake at the time of collection. In order to show values for these three items in table 3 for a period *similar* to that between September 16, 1950, and June 21, 1951, the determinations made by Miller (1936) on comparable dates in 1933 and 1934 are included.

Temperatures.—On June 24, 1948, when this investigation was begun on Douglas Lake, thermal stratification was already in process (table 1). A

vertical temperature series demonstrated that the upper limit of the thermocline occurred at 11 meters and the lower limit at 13 meters. As the season progressed, the thermocline gradually descended and on August 12, when work terminated for the summer, it occupied the stratum of water between 14 and 16 meters. At no time during this period did the thickness of the thermocline become less than three or greater than four meters.

TABLE 1.—Physico-chemical data from Douglas Lake during the summer of 1948

	Water temperatures in degrees Centigrade (Depth in meters)											
	0	10	11	12	13	14	15	16	17	18	19	20
Jun. 24	19.9	16.7[	....	14.3	....	]13.0	....	12.2	....	11.3	....	10.8
Jul 1	19.7	18.4	....	[18.4	....	14.3	....	]12.8	....	11.8	....	10.9
Jul 8	22.4	19.9	....	[17.4	15.0	13.0	....	]12.0	....	....	....	10.8
Jul 15	24.6	19.9	....	[17.7	....	13.9	....	]12.1	....	11.4	....	10.9
Jul 22	22.7	20.3	....	[17.4	....	13.6	....	]12.2	....	11.5	....	10.8
Jul 29	23.1	20.6	....	20.0[	....	17.3	....	12.3]	....	11.5	....	10.8
Aug 5	21.8	20.8	....	20.6	....	[18.8	....	12.6]	....	11.6	....	10.8
Aug 12	20.1	19.9	....	19.6	....	[19.0	....	12.9]	....	11.4	....	10.6

	Carbonates ppm						Bicarbonates ppm				
	0	3	5	10	20		0	3	5	10	20
Jun. 24	0	0	0	0	0		109	110	110	111	112
Jul 1	5	2	2	2	0		110	111	115	117	121
Jul 8	3	....	4.2	1.6	0		113	....	114	117	121
Jul 15	6	....	2	0	0		115	....	119	122	122
Jul 22	6	....	4	4	0		112	....	114	114	122
Jul 29	8	....	8	8	0		114	....	114	116	130
Aug 5	12	....	....	14	0		111	....	....	111	132
Aug 12	10	....	....	12	0		113	....	....	113	133

	pH						Oxygen ppm				
	0	3	5	10	20		0	3	5	10	20
Jun. 24	8.0	8.0	8.0	7.7	7.2		7.6	7.4	6.9	6.2	0.3
Jul 1	8.2	8.2	8.2	8.2	7.3		7.5	7.8	7.5	6.9	0.8
Jul 8	8.2	8.2	8.2	8.2	7.3		7.4	....	7.1	6.0	0.6
Jul 15	8.4	....	8.2	8.0	7.3		7.6	....	7.0	4.8	0.6
Jul 22	8.3	....	8.3	8.0	7.2		7.3	....	7.3	5.8	0
Jul 29	8.3	....	8.3	8.2	7.1		7.6	....	7.2	6.7	0
Aug 5	8.4	....	....	8.1	7.1		6.5	....	....	6.7	0
Aug 12	8.4	....	....	8.1	7.1		6.7	....	....	6.4	0

	Carbon dioxide ppm				
	0	3	5	10	20
Jun. 24	0	0	0	0.2	1.0
Jul 1	0	0	0	0	0.5
Jul 8	0	0	0	0	0.7
Jul 15	0	0	0	0	1.0
Jul 22	0	....	0	0	1.0
Jul 29	0	....	0	0	1.5
Aug 5	0	....	0	0	1.0
Aug 12	0	....	0	0	1.0

Thermoclines enclosed in brackets

The investigation was resumed on July 3, 1950, and on this day the thermocline occurred between 13 and 16 meters (table 2). By September 16, 1950, its upper limit had been pushed down to 16 meters and its lower limit to 18 meters, a distance of only two meters from the bottom. On October 2, a vertical temperature series demonstrated a homothermous condition in the lake and on November 24, ice first appeared. The ice began to break up on April 13, 1951, but there was still no thermal stratification on May 10. On May 25, however, the lake was definitely stratified so it appears that stratification must have begun sometime between May 10 and May 25. On the latter date, incidentally, the upper limit of the thermocline was already at 12 meters. No temperature series were taken between these two dates so that the actual rate of descent of the thermocline cannot be determined. It is interesting to note that it did occur during a period of 15 days. As a matter of fact, in none of the temperature series taken during the 16 months of collection in Douglas Lake was the upper limit of the thermocline ever found to be above ten meters.

From May 10 to September 15, 1951, the lake remained thermally stratified, the vertical temperature series being very similar to those of the previous year. By October 6 the lake was once again homothermous. The latter phenomenon occurred at approximately the same time during the year before.

The temperature data collected during each of the summers of 1948, 1950 and 1951 do not differ markedly from each other, neither do they differ greatly from data collected by Welch and Eggleton during other summers. It is interesting to compare the temperature data collected by the present writer between July 3, 1950, and October 6, 1951, with those collected by Miller 17 years previously between September, 1933, and August, 1934. During both of these periods of investigation, thermal stratification began on approximately the same date. Furthermore, the lake became *homothermous* at almost the same time in each of the two periods. Also, ice appeared at about the same day during both periods and persisted for similar lengths of time in both cases.

Conductivity.—During the summer of 1948, these determinations were made along with other routine analyses. On June 24 the conductivity was 220 mhos through the entire depth of the lake. As a matter of fact, none of the determinations made during the early and middle part of the summer varied more than five reciprocal megohms from this reading. On August 5, towards the end of the summer, the conductivity still remained the same in the upper 17 meters, however it had increased to 225 and 235 at 18 and 20 meters respectively. During the summers of 1950 and 1951 conductivity determinations were not made as frequently, but those that were made indicated that these summers were not very different from that of 1948. Determinations made by Welch and Eggleton during previous summers were also very similar to those of the present investigation.

Oxygen.—The oxygen content of Douglas Lake varies through the seasons as it does in any other temperate lake of the second order (tables 1 and 3). During the periods of thermal stratification, oxygen is distributed uniformly throughout the epilimnion. In the hypolimnion, oxygen decreases as the summer progresses and disappears completely from the bottom several months

TABLE 2.—Seasonal and vertical temperature series in Douglas Lake 1950-1951

Water temperatures in degrees Centigrade

(Depth in meters)

	0	10	11	12	13	14	15	16	17	18	20
1950 Jul. 3	18.5	17.8	---	17.8	[17.3]	13.5	9.6	8.2]	7.5	---	6.6
Jul. 10	22.8	---	---	18.1	[17.7]	16.5	12.1	9.4]	---	7.8	6.8
Jul. 18	20.6	---	---	18.8	---	17.4	12.7	10.0]	---	8.2	7.0
Jul. 25	21.2	---	---	---	---	17.4	14.6	10.4	8.6]	---	6.9
Aug. 4	20.6	---	---	17.9	---	[---	---	7.5]	---	---	6.8
Aug. 14	20.0	---	---	[18.8	17.8	15.1	10.9	8.4	7.1]	---	6.8
Aug. 31	17.0	16.5	---	---	---	[16.5	14.5	9.0	7.5]	7.0	7.0
Sep. 16	15.0	---	---	14.0	---	---	---	[14.0]	11.0]	8.0]	7.0
Oct. 2a	14.5	13.0	---	12.5	---	12.5	12.5	12.5	12.0	11.5	11.5
Oct. 19	12.0	12.0	---	11.5	---	---	11.5	---	11.5	11.5	11.5
Nov. 14	4.5	---	---	---	---	---	---	---	---	---	4.5
Dec. 27b	0.0	1.0	---	---	---	---	---	---	---	---	2.5
1951 Feb. 26	1.0	2.0	---	---	---	---	---	---	---	---	3.0
Mar. 28	0.0	0.5	---	---	---	---	---	---	---	---	2.5
Apr. 23c	4.5	---	---	---	---	---	---	---	---	---	4.5
May 10	8.0	10.0	---	[11.0	9.0	6.0	---	---	---	---	4.5
May 25d	16.0	12.0	---	[12.5	9.5	7.5	7.5	---	---	---	5.0
Jun. 8	16.5	14.5	---	13.0	---	7.5	7.0	7.0	6.0	5.0	5.0
Jun. 21	19.0	16.0	[---	---	---	8.0	---	7.3]	---	5.0	5.5
Jul. 9	19.7	---	---	[17.1	11.7	9.4	---	7.9	6.7]	5.0	5.9
Jul. 23	20.5	19.5	[19.2]	17.7	13.4	9.6	8.3	7.5]	7.3	5.5	6.1
Aug. 10	21.5	20.7	---	[19.9	13.4	11.2	8.6]	8.2]	---	6.3	6.3
Aug. 25	20.3	19.0	---	18.8	[18.4	14.4	8.6	8.5	7.6	6.9	6.7
Sep. 15	17.9	---	---	---	17.5	16.4	10.1	---	7.5]	7.0	6.8
Oct. 6e	12.8	---	---	12.0	---	---	14.2	---	---	---	11.8

Thermoclines enclosed in brackets
a Fall overturn began between Sept. 16 and Oct. 2, 1950
b Ice appeared Nov. 24, 1950
c Ice disappeared April 13, 1951
d Thermal stratification began between May 10 and May 25, 1951
e Fall overturn began between Sept. 15 and Oct. 6, 1951

TABLE 3.—Seasonal and vertical distribution of certain chemical factors in Douglas Lake 1950-1951

(Depth in meters)

Date	Carbonates ppm					Bicarbonates ppm					pH					Oxygen ppm					Free Carbon Dioxide				
	0	2	5	12	20	0	2	5	12	20	0	2	5	12	20	0	12	16	18	20	0	12	16	18	20
1950 Jul 3	10	---	8	0	0	118	---	120	128	131	8.4	---	8.3	8.1	7.1	7.8	7.4	5.8	3.1	1.3	0	0	5.6	8.4	11.0
Jul 10	6	---	12	0	0	122	---	115	127	131	8.2	---	8.2	8.1	7.0	7.8	7.2	5.6	2.9	1.3	0	0	7.1	9.8	12.5
Jul 18	12	---	12	0	0	112	---	112	131	132	8.3	---	8.3	8.1	7.0	7.5	6.8	0.9	---	0	0	0	11.0	---	11.0
Jul 25	8	---	12	0	0	118	---	114	124	129	8.3	---	8.3	8.1	7.0	7.4	6.3	0.3	0.1	0	0	0	8.4	11.2	13.1
Aug 4	8	---	12	0	0	106	---	108	124	132	8.3	---	8.3	8.1	7.0	8.7	7.5	0.1	---	0	0	0	8.8	---	14.0
Aug 14	6	---	6	0	0	118	---	120	128	131	8.2	---	8.0	7.9	7.0	8.6	6.8	---	---	0	0	1.4	---	---	16.0
Aug 31	6	---	4	8	0	124	---	126	131	138															
Sep 16	3	3	8	8	0	122	122	117	117	136	8.4	---	---	---	6.9	8.5	---	3.7	1.3	0	0	---	4.0	7.0	15.0
Oct 2a	6	8	2	2	0	118	117	123	125	130	8.1	---	---	---	7.7	9.6	---	---	---	8.7	0	---	---	---	0
Oct 19	8	8	2	2	0	118	119	125	126	131															
Nov 14	7	8	2	2	0	119	118	124	127	129	8.2	---	---	---	8.2	12.0	---	---	---	11.0	0	---	---	---	0
Dec 27b	0	---	0	0	0	122	---	127	130	136															
1951 Feb 26	0	---	0	0	0	31	---	129	131	141	7.7	---	---	---	7.1	13.0	---	---	1.4	0.7	0	---	---	---	3.0
Mar 28	0	---	0	0	0	26	---	128	132	138	7.3	---	---	---	6.9	10.0	---	---	1.7	0.4	1	---	---	---	12.0
Apr 23c	0	---	0	0	0	110	---	112	114	119	7.3	---	---	---	7.3	9.0	---	---	---	9.4	1	---	---	---	2.0
May 10	0	---	0	0	0	109	---	113	113	118	7.8	---	---	---	7.3	11.0	10.5	---	---	9.4	0	1	---	---	2.0
May 25d	0	---	1	0	0	110	---	116	117	119	8.1	---	---	7.6	7.2										
Jun 8	1	---	1	0	0	116	---	118	118	120	8.1	---	---	7.9	7.1	7.7	7.2	---	---	1.0	0	0	---	---	5.0
Jun 21	1	---	1	0	0	119	---	120	120	121	8.1	---	---	7.4	6.9	8.2	5.7	---	---	0	0	2	---	---	10.0
Jul 9	6	6	6	0	0	117	---	118	121	122	8.3	8.3	8.3	7.9	7.1	8.2	7.0	1.4	0.3	0	0	3	---	---	14.5
Jul 23	6	6	6	0	0	115	---	---	122	130	8.2	8.2	8.2	7.6	7.0	8.0	4.2	0.1	---	0	0	6	11.9	---	15.5
Aug 10	8	---	7	1	0	112	---	---	119	129	8.2	---	---	8.0	7.1	8.7	5.5	0.4	---	0	0	6	16.0	---	17.0
Aug 25	5	4	2	5	0	114	---	119	122	131	8.3	---	---	8.1	7.0	8.6	5.4	0.1	0	0	0	0	0	0	17.0
Sep 25	5	4	2	2	0	117	---	119	123	133	8.3	---	---	8.0	7.1	8.8	5.8	1.4	0	0	0	0	0	0	18.0
Oct 6e	8	9	3	0	0	117	---	119	122	124	8.1	---	---	7.8	7.8	9.2	---	---	---	8.7	0	0	0	0	2.0

The data surrounded by brackets were taken from the data of D. E. Miller (1936). These determinations were made by Miller on comparable dates in 1933-1934.

(a), (b), (c), (d), (e)—See footnotes for table 2.

before the autumnal overturn, but during this overturn it is recirculated throughout the whole lake. In the winter, under the ice cover, the bottom waters again become depleted of dissolved oxygen and remain thus until the spring overturn. It is of interest to compare the dates in the different summers when oxygen disappeared from the bottom waters in Douglas Lake. The following list presents these data and indicates by whom they were collected.

Dates of Disappearance		Author	Published
Between July 21 and 27	1923	Eggleton	1931
Before July 1	1926	Eggleton	1931
Between July 6 and 27	1927	Eggleton	1931
Before July 27	1928	Eggleton	1931
Before July 21	1933	Eggleton	1931
Between June 2 and 16	1934	Miller	1936
Between July 15 and 22	1948	Tucker	(Herein)
Between July 18 and 25	1950	Tucker	(Herein)
Before July 9	1951	Tucker	(Herein)

Evidently when the summer investigations were begun in 1926, 1928, 1933 and 1951, the oxygen was already absent from the bottom and, hence, the actual time of disappearance cannot be stated.

As far as the writer is aware, only one paper (Miller, 1936) has been published which contains continuous data on dissolved oxygen in Douglas Lake during the winter months. According to his records for the year 1934, oxygen began to decrease from the bottom waters soon after the ice cover appeared. It never completely disappeared but reached the low value of 0.4 ppm during the latter part of March. Miller had no oxygen records for the period between this date and April 29 at which time the spring overturn was taking place. It could very well be that between these dates the oxygen might have disappeared completely from the bottom.

Hydrogen Ion Concentration (tables 1 and 3).—Generally speaking, it may be stated that during the thermal stratification periods in 1948, 1950 and 1951, the pH nearly always varied between 8.0 and 8.4 in the epilimnion and between 7.0 and 8.0 in the hypolimnion, decreasing, of course, from surface to bottom but, nevertheless, demonstrating chemical stratification. No pH data were collected by the writer for the interim between the fall overturn in 1950 and the spring overturn in 1951. According to the records of Miller (1936), the pH during the fall overturn in 1933 was 8.2 throughout the entire depth, but under the ice on April 7, 1934, it decreased to 7.3 at the surface and 6.9 at the bottom. During the circulation in the spring overturn it was 7.3 from surface to bottom.

Free Carbon Dioxide (tables 1 and 3).—During the summers of 1948, 1950 and 1951, analyses showed no evidence of free carbon dioxide in the epilimnion at any time. At the bottom of the hypolimnion, during the summer of 1948, the amounts ranged between 0.5 to 1.5 ppm. During the summers of 1950 and 1951 the values in the upper limits of the hypolimnion fluctuated between 5.6 and 16.0 ppm, whereas at the lower limit they occurred in amounts ranging between 11.0 and 18.0 ppm; the general trend being towards an increase as the summer progressed.

No data on carbon dioxide were secured during the time between the fall

overturn of 1950 and the spring overturn of 1951. Miller's data show, however, that during the fall overturn of 1933, when the pH was 8.2 from surface to bottom, there was no free carbon dioxide throughout the entire depth, but at the beginning of April, 1934, under the ice cover, the surface and bottom waters contained 1.0 ppm and 12.0 ppm respectively. During the spring overturn of the same year, shortly after the ice had broken up, the amount of free carbon dioxide throughout the whole depth was between 1.0 and 2.0 ppm.

Carbonates (tables 1 and 3)—The data collected during the summers of 1948, 1950 and 1951 showed that the carbonate content of the epilimnion waters occurred in amounts between 0.0 and 14.0 ppm. The difference between the amounts of carbonate present in the upper and lower limits of the epilimnion at any one time never exceeded 6.0 ppm. None of the water samples collected in the hypolimnion waters contained any trace of carbonates. After the fall overturn in September, 1950, carbonates still persisted in the upper waters until the ice appeared in amounts ranging between 2.0 and 8.0 ppm, but at the 20-meter depth carbonates were never found. As a matter of fact, they were never found in any of the water samples collected at that depth during the entire time of the investigation. Under the ice cover carbonates did not appear in any of the samples from any of the depths, but small traces appeared again soon after the ice broke up in April, 1951.

Bicarbonates (tables 1 and 3; fig. 1).—The data from the summer of 1948 showed that in the upper limit of the epilimnion, the amounts of bicarbonates fluctuated between 109 ppm and 115 ppm and in the lower limit between 111 ppm and 122 ppm. In all cases, the difference between the bicarbonate content of the upper and lower limits of the epilimnion at any one time never exceeded 7.0 ppm. At the 20-meter depth, the quantities of bicarbonate increased progressively from 112 ppm on June 24 to 133 ppm on August 12.

Fig. 1 shows the quantitative seasonal variations of bicarbonates at depths of 5 meters and 20 meters during the 16 consecutive months of investigation from September, 1950, to October, 1951. The changes at these depths were arbitrarily chosen to represent the changes occurring in the epilimnion and hypolimnion respectively. Between July 3 and August 4, 1950, at the 5-meter depth, there was a decrease from 120 ppm to 108 ppm. From the latter date to August 31 the bicarbonate content increased to 126 ppm. On September 16, the first sampling day during the fall overturn, it was down to 117 ppm. By October 19 it had reached a value of 125 ppm. It changed very little during the next five months even during the time of the ice cover, and on March 28, 1951, still under the ice cover, bicarbonates were present in the amount of 128 ppm. On April 23, the first day of sampling after the ice had disappeared, there were present only 112 ppm, the decrease undoubtedly having occurred during the spring overturn. This is a repetition of the phenomenon occurring during the preceding fall overturn because then, too, there was a marked decrease. From April 23 to October 6 there was a gradual increase to 119 ppm.

At the 20-meter depth, from June 3 to August 14, 1950, the amounts of bicarbonate present fluctuated between 129 ppm and 131 ppm, however by August 31 the bicarbonate content had increased to 138 ppm. About two
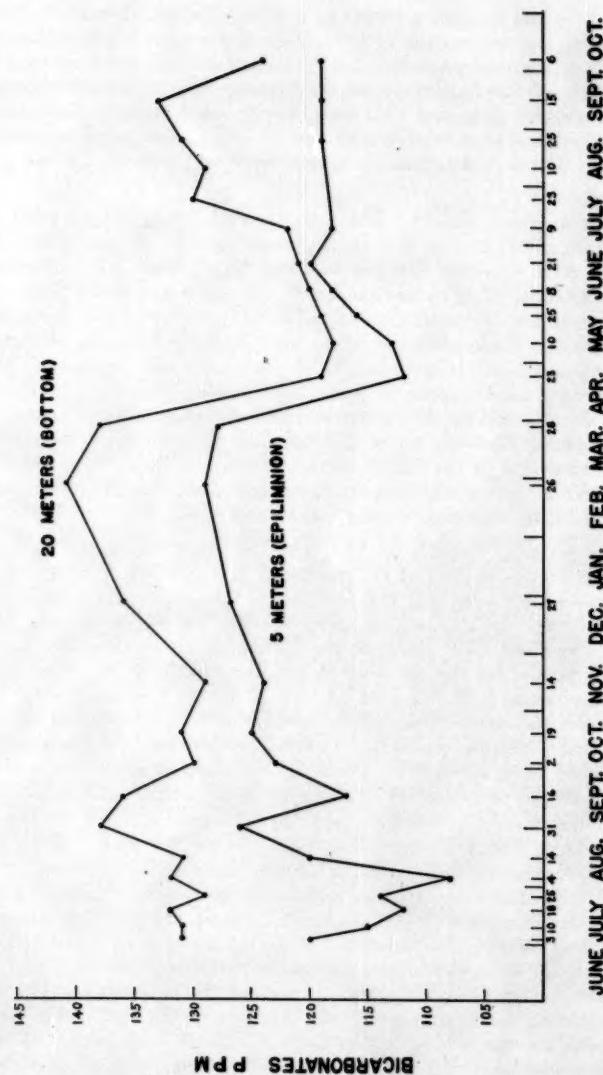
Fig. 1.—Variation in bicarbonates in Douglas Lake (South Fishtail Bay), years 1950-1951. Fall overturn began between Sept. 16 and Oct. 2, 1950; ice appeared Nov. 24, 1950; ice disappeared April 13, 1951; thermal stratification began between May 10 and May 25, 1951; fall overturn began between Sept. 15 and Oct. 6, 1951.

weeks later, on September 16 it was 136 ppm but after the beginning of the fall overturn, that is the period between September 16 and October 2, it decreased to 130 ppm and remained approximately at this value until the ice cover appeared. Under the ice it increased quite markedly as was indi-

TABLE 4.—Seasonal and vertical distribution of phosphorus in Douglas Lake 1950-51 (Values of the total and the various fractions of phosphorus are reported in the body of the table as micrograms per liter)

		Phosphorus																				
		Total							Soluble Inorganic							Total Organic						
		Depth in meters																				
		0	2	5	12	16	18	20	0	2	5	12	16	18	20	0	2	5	12	16	18	20
1950	Jul. 3	8	8	9	8	12	13	13	2	2	1	1	2	2	3	6	6	8	7	10	11	10
	Jul. 7	8	9	8	9	9	9	12	2	1	1	0	2	1	2	6	8	7	7	9	8	10
	Jul. 10	8	7	9	9	10	11	13	1	1	2	2	3	3	4	7	6	7	9	7	8	9
	Jul. 14	8	8	9	10	13	14	14	0	1	1	2	1	3	3	8	7	8	8	12	12	11
	Jul. 18	8	8	8	7	10	10	15	1	1	1	1	2	2	2	7	7	7	6	8	8	8
	Jul. 25	8	13	11	12	11	....	15	1	1	1	1	1	....	2	7	12	10	11	10	....	13
	Aug. 4	7	8	7	9	9	9	14	1	0	0	1	1	....	2	6	8	7	9	8	....	12
	Aug. 14	14	13	15	15	9		17	0	1	1	1	1		1	14	12	14	7	8		16
	Aug. 31	8	9	12	9			50	2	1	1	2			18	6	8	11	7			32
	Sep. 16	9	9	9	8			641	3	5	3	6			460	6	6	6	6			181
	Oct. 2a	9	9	11	10			22	3	6	3	6			12	4	3	4	4			10
	Oct. 19	11	12	11	10			13	4	5	4	5			6	7	7	7	5			7
	Nov. 14	10	10	10	9			8	6	3	6	5			4	4	7	4	4			4
	Dec. 27b	9	11	11	11			43	2	3	2	3			31	7	8	9	8			12
1951	Feb. 26	11	11	10	12			48	4	3	6	4			33	7	8	4	7			15
	Mar. 28	12	13	11	12			27	3	3	4	4			15	9	10	7	8			12
	Apr. 23c	9	9	8	9			10	2	2	2	2			2	7	8	6	7			8
	May 10	9	9	8	9			12	2	2	2	1			1	7	7	7	8			11
	May 25d	7	8	9	9			11	1	2	1	1			2	6	6	7	8			9
	Jun. 8	9	9	10	9			12	2	1	3	2			3	7	8	6	8			9
	Jun. 21	7	9	9	7			12	1	2	2	2			3	6	7	7	6			10
	Jul. 9	8	9	9	9			10	1	1	2	1			2	7	8	7	7			8
	Jul. 23	9	8	9	9			12	1	1	1	1			3	8	7	8	8			9
	Aug. 10	10	8	10	8	10	10	14	1	1	1	1	1	1	4	9	7	9	7	9	9	10
	Aug. 25	9	8	11	9	10	11	12	1	1	1	1	1	1	1	8	7	10	8	9	9	9
	Sep. 15	10	9	11	10	9	10	34	1	1	1	1	1	3	20	9	8	10	9	8	8	14
	Oct. 6e	12	11	10	9	9	10	12	2	2	1	1	1	1	2	10	9	9	8	8	9	10

TABLE 4.—(continued)

		Phosphorus													
		Sestonic							Soluble Organic						
		Depth in meters													
		0	2	5	12	16	18	20	0	2	5	12	16	18	20
1950 Jul 3		5	4	4	5	3	4	5	1	2	4	2	7	7	5
Jul 7		4	4	4	5	2	4	5	2	4	3	4	7	4	5
Jul 10		2	2	2	4	4	6	6	5	4	5	3	3	2	3
Jul 14		2	2	1	3	5	6	5	6	5	7	6	7	6	6
Jul 18		5	....	4	3	4	4	5	2	....	3	3	4	4	3
Jul 25		2	6	3	6	4	....	1	5	6	7	5	6	....	12
Aug 4		2	3	4	4	4	....	3	5	5	3	5	4	....	9
Aug 14		3	4	9	7	....	....	7	11	8	5	7	....	....	9
Aug 31		2	4	5	5	....	....	30	4	4	6	2	....	....	2
Sep 16		2	2	2	2	....	....	159	4	4	4	4	....	....	22
Oct 2a		3	3	2	3	....	....	10	1	0	2	1	....	....	0
Oct 19		3	2	4	2	....	....	4	4	5	3	3	....	....	3
Nov 14		2	1	1	1	....	....	1	2	3	2	3	....	....	3
Dec 27b		2	3	4	3	....	....	7	5	4	4	5	....	....	5
1951 Feb 26		3	2	1	3	....	....	7	4	6	5	4	....	....	8
Mar 28		3	3	4	4	....	....	6	6	7	3	4	....	....	6
Apr 23c		2	3	2	1	....	....	2	5	5	5	6	....	....	6
May 10		2	2	1	2	....	....	3	5	5	6	6	....	....	8
May 25d		2	2	2	3	....	....	3	4	4	5	5	....	....	6
Jun 8		2	3	2	1	....	....	4	5	3	6	6	....	....	6
Jun 21		1	2	2	2	....	....	3	5	6	5	4	....	....	6
Jul 9		2	1	3	2	....	....	4	5	6	5	5	....	....	4
Jul 23		2	3	2	1	....	....	4	6	4	6	7	....	....	5
Aug 10		2	3	2	3	....	....	5	7	5	7	4	....	....	5
Aug 25		1	2	2	1	2	3	3	7	5	8	7	7	6	7
Sep 15		2	1	3	2	2	3	8	7	7	7	8	7	5	6
Oct 6e		3	1	2	1	1	1	1	7	8	7	7	7	8	9

(a), (b), (c), (d), (e)—See footnotes for table 2.

cated by the 136 ppm of bicarbonate present on December 27. The bicarbonates continued to increase in quantity under the ice, reaching a maximum value of 141 ppm on February 26, 1951, but still being present in the amount of 138 ppm on March 28. Sometime between March 28 and April 23 the ice broke up and the spring overturn began. During this period the bicarbonates decreased to 119 ppm which was the amount found on the latter date. From this day to July 9 there was never a greater variation than 2.0 ppm from this amount one way or the other. However, between July 9 and July 23 it had increased in quantity to 130 ppm. It remained between 129 ppm and 133 ppm until the fall overturn which occurred between September 25 and October 2, for on the latter date the bicarbonate content was 124 ppm.

Phosphorus (table 4; figs 2, 3, 4 and 5).—At the beginning of the summer of 1950 it was decided to make phosphorus analyses every two or three days in order to observe what kind of changes occur during short periods of time. This procedure was carried on for about three weeks but no significant changes were observed after such short periods of time. For this reason

samples were collected and phosphorus determinations made at approximate two-week intervals thereafter.

During the 16 months of investigation, at the surface the amounts of total phosphorus fluctuated between 7 and 14 micrograms per liter. At the 12-meter depth, which was the average depth of the lower limit of the epilimnion during stratification, the amounts varied between 7 and 15 micrograms per liter. The actual difference between the maximum and minimum amounts in the upper 12-meter stratum at any one time never exceeded four micrograms per liter (fig. 2). The fluctuations which occurred in this stratum during the 16-month period were quite irregular and seemed to follow no particular trend which could be related either to the chronological or limnological seasons. At the 20-meter depth, however, (fig. 4) a different phenomenon occurred. Between July 3 and August 4, 1950, there were irregular fluctuations in amounts of total phosphorus varying between 10 and 17 micrograms per liter. On August 31, about four or five weeks after the oxygen had disappeared from this depth, the amount of total phosphorus present was 50 micrograms per liter and by September 16 it had reached the enormous value of 641 micrograms per liter. On October 2 during the fall overturn it was down again to 22 micrograms per liter and did not exceed this value until the ice cover had formed, after which time it continually increased until sometime between February 26 and March 28. The highest value obtained during the winter was 46 micrograms per liter which was the amount of total phosphorus found on February 26, 1951. By April 23, about 10 days after the ice had broken up, a noticeable decrease had taken place. By that date, the value had dropped to 10 micrograms per liter. Indeed, from April 13 through August 25 the amounts never exceeded 14 micrograms per liter. Between August 23 and September 15, however, approximately eight weeks after oxygen depletion from the bottom, the total phosphorus content increased. On the latter date it was found to be present in the amount of 34 micrograms per liter. During the overturn, two weeks later, it was down again to 12 micrograms per liter.

In general, the seasonal variations in the soluble inorganic phosphorus were almost identical with the total phosphorus variations but in lesser quantities. In the top 12-meter stratum the amounts of soluble inorganic phosphorus fluctuated between 0.0 and 7.0 micrograms per liter throughout the entire 16-month investigation. The difference between the maximum and minimum values on any one day, however, never exceeded 2.0 micrograms per liter (fig. 3). At the bottom (fig. 4) the amounts of soluble inorganic phosphorus ranged between 1.0 and 4.0 micrograms per liter from July 3, 1950, to August 14, increasing to 18 micrograms per liter by August 31 and eventually to 460 micrograms per liter by September 15. During the autumnal overturn the soluble inorganic phosphorus decreased to values between 4 and 12 micrograms per liter but under the ice it began to increase again reaching its highest value on February 26, 1951, at which time it was 33 micrograms per liter. It began to decrease even before the ice had broken up, but a marked decrease was not observed until the ice had disappeared and the spring overturn was in progress. At this time, April 23, it was present in the amount of 2.0 micrograms per liter and it changed very little from this
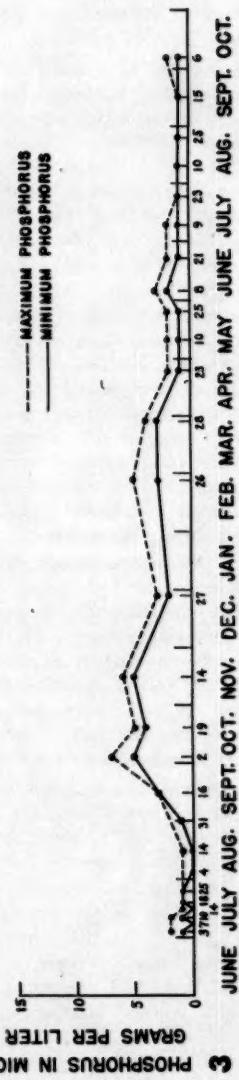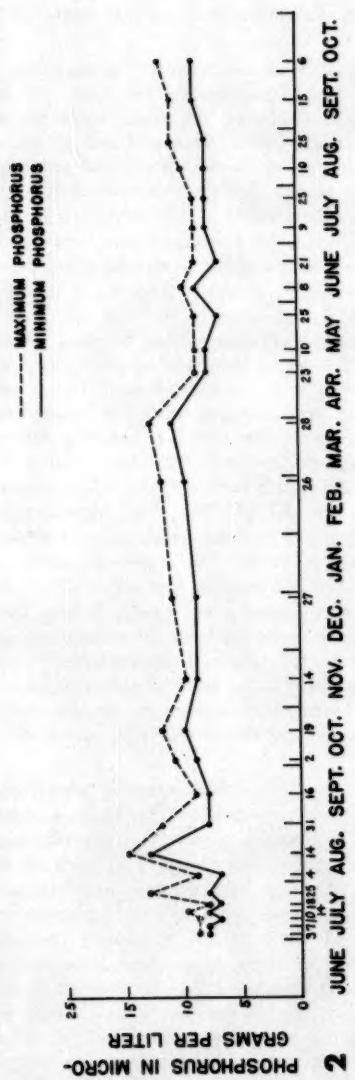
Figs. 2, 3.—Maximum and minimum values of phosphorus occurring between surface and 12-meter depth in Douglas Lake (South Fishtail Bay), years 1950-1951. 2. Total phosphorus; 3. Soluble inorganic phosphorus. See explanation of fig. 1. —

value until sometime between August 24 and September 15, 1951, but on the latter date it was 20 micrograms per liter. On October 2, 1951, during the autumnal overturn it was once again down to the small value of 2.0 micrograms per liter.
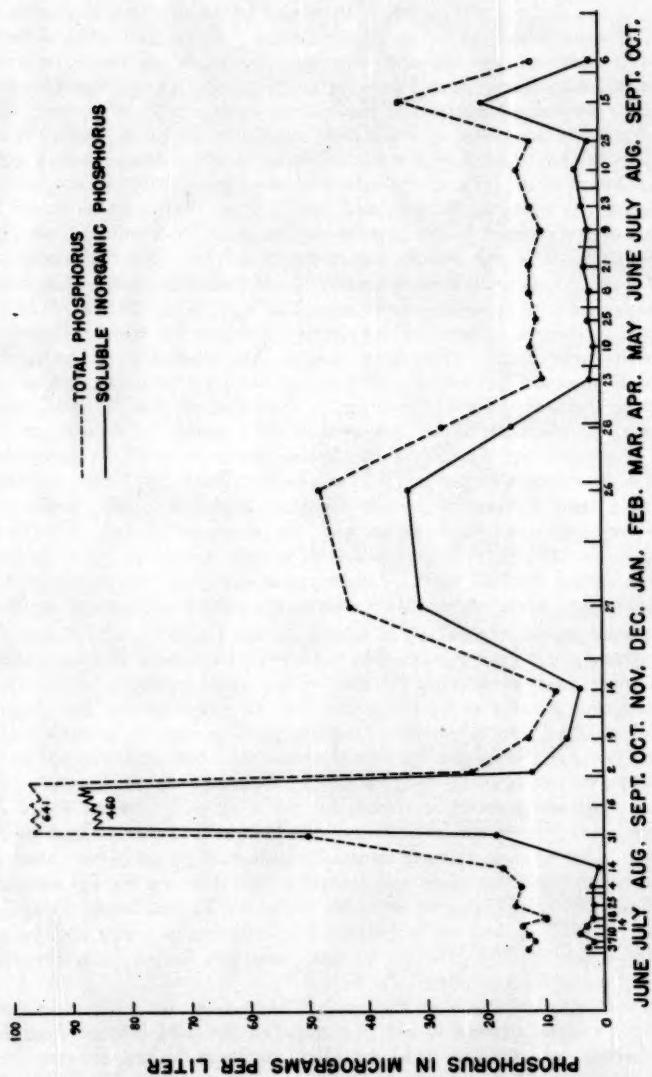
Fig. 4.—Variations of total phosphorus and soluble inorganic phosphorus at 20-meter depth in Douglas Lake (South Fishtail Bay), years 1950-1951. See explanation of fig. 1.

During the first few months of the investigation in Douglas Lake starting on July 3, 1950, vertical series of phosphorus determinations were made at close depth intervals, only down to 12 meters which was the lower limit of the epilimnion. Frequent determinations were made only in this stratum

because it included the photosynthetic zone and information was desired as to the phosphorus available to the phytoplankton. Each time when a series was taken, however, one determination was also made on the water from the bottom, more for the record than for anything else, but no determinations were made between 12 meters and the bottom which was at 20 meters. The latter depth was the lowest at which clear samples could be obtained. When the results of the analyses on the bottom water samples showed such a great increase several weeks prior to the autumnal overturn of 1950, it was decided that during the following summer and early fall of 1951, samples would be collected at every meter in the hypolimnion in order to determine how high the phosphorus from the bottom waters would diffuse. This was done and table 7 and fig. 5 show the vertical distribution of soluble inorganic phosphorus in Douglas Lake on successive dates from July 9, 1951, to October 6 of the same year. Samples collected at 20 meters were clear but those collected at 20.5 meters were muddy. The latter samples were allowed to set for several hours until the mud had settled and the clear water in the upper part of the bottle was analyzed. Table 7 and fig. 5 show that on July 9, 1951, there were only 4.0 micrograms per liter even at 20.5 meters. However, as the season progressed the amount at the bottom increased until on September 15 it was 80 micrograms per liter. It can be seen from fig. 3 that, although this was a large increase in soluble inorganic phosphorus, still it did not diffuse very high into the hypolimnion. As a matter of fact, it diffused only up to the 18-meter depth, a distance of a mere two meters. On October 6, a day during the fall overturn, the soluble inorganic phosphorus at the bottom was once again among its low values, this time 8 micrograms per liter.

The total organic phosphorus in Douglas Lake (table 4), also underwent quantitative changes from time to time during the 16 months of investigation. In the upper 12-meter stratum, however, it was never found to be less than 4.0 micrograms per liter and never greater than 11 except on one day, August 14, 1950, at which time it was 14 micrograms per liter both at the surface and at 12 meters. The difference between the maximum and minimum values in this stratum on any one day never exceeded 5.0 micrograms per liter. At the 20-meter depth the amount fluctuated, for the most part, between 4 and 11 micrograms per liter except for short periods just prior to the fall and spring overturns. During these times it increased much more in some years than in others. For example, the maximum amount recorded before the fall overturn in 1950 was 181 micrograms per liter, but under the ice just before the spring overturn of 1951, it had reached only 15 micrograms per liter and before the fall overturn of 1951, after the summer minimum, it had again increased only to 14 micrograms per liter.

The sestonic phosphorus in the upper 12-meter stratum always occurred in amounts ranging between 1 and 9 micrograms per liter. At no time did the difference between the maximum and minimum values for any one vertical series exceed 4 micrograms per liter. At the 20-meter depth the amounts fluctuated between 1 and 10 micrograms per liter, except during the period before the fall overturn in 1950. During this period it reached the high value of 159 micrograms per liter but this amount decreased to the usual range during the overturn. It did not increase markedly before the

TABLE 5.—Physico-chemical data from Lancaster Lake during the summers of 1948-1950-1951

Water temperatures in degrees Centigrade — Depth in meters

Date	0	1	2	3	4	5	6	7	15
1948 Jul 5	23.9	---	[23.7	17.5	11.2	8.8	6.9	6.3	5.0
Jul 12	26.2	25.8	[25.0	17.2	12.5	9.0	7.6	6.5]	5.0
Jul 19	23.2	23.2	23.0	[23.0	12.8	9.2	7.3	6.6	5.0
Jul 26	20.4	20.3	20.3	20.1	12.6	9.0	7.3	6.8	5.2
Aug 2	21.2	---	21.2	21.0	15.4	9.0	7.7	6.8	5.0
Aug 9	20.1	---	20.0	20.0	15.7	8.9	7.5	6.7	5.0
1950 Jul 20	20.1	---	[19.6	12.4	9.4	7.8]	7.3	6.8	5.8
Aug 8	21.6	---	[18.2	14.2	9.7	7.9]	7.0	---	5.8
1951 Jul 20	19.7	[19.3	13.8	9.0	5.9]	---	5.2	---	4.7
Aug 16	21.2	[19.4	12.0	8.1	6.3	5.5	---	---	4.8
Aug 25	21.0	18.4	13.1	8.0	6.1	5.8	---	---	4.9
Sep 15	17.7	17.7	16.5	9.3	6.2	5.8	---	---	4.9

Carbonates ppm

Date	0	2	6	15
1948 Jul 5	4	14	0	0
Jul 12	4	8	0	0
Jul 19	8	12	0	0
Jul 26	6	12	0	0
Aug 2	7	8	0	0
Aug 9	4	8	0	0
1950 Jul 20	4	4	0	0
Aug 8	0	4	0	0
1951 Jul 20	0	0	0	0
Aug 16	3	0	0	0
Aug 25	4	3	0	0
Sep 15	4	4	0	0

pH — Depth in meters

Date	0	2	6	15
1948 Jul 5	8.0	8.0	7.2	7.1
Jul 12	8.0	8.0	7.2	7.2
Jul 19	8.2	8.2	7.3	7.3
Jul 26	8.2	8.2	7.2	7.2
Aug 2	8.2	8.2	7.3	7.3
Aug 9	8.3	8.2	7.2	7.2
1950 Jul 20	8.1	8.1	7.2	7.1
Aug 8	7.8	7.3	7.2	7.2
1951 Jul 20	8.0	7.6	7.1	7.1
Aug 16	8.0	8.0	7.1	7.1
Aug 25	8.1	8.0	7.1	7.1
Sep 15	8.2	8.2	7.1	7.1

Carbon dioxide ppm

Date	0	2	6	15
1948 Jul 5	0	0	7	11
Jul 12	0	0	8	10
Jul 19	0	0	10	12
Jul 26	0	0	12	13
Aug 2	0	0	11	12
Aug 9	0	0	12	13
1950 Jul 20	0	0	8	12
Aug 8	2	0	7	10
1951 Jul 20	2	2	8	12
Aug 16	0	2	9	15
Aug 25	0	2	11	16
Sep 15	0	0	13	19

Bicarbonates ppm

Date	0	1	2	6	15
1948 Jul 5	134		122	151	195
Jul 12	134		134	171	203
Jul 19	128		128	149	182
Jul 26	122		120	139	188
Aug 2	138		137	168	198
Aug 9	136		134	150	200
1950 Jul 20	150		152	169	178
Aug 8	152		153	158	180
1951 Jul 20	138		146	155	199
Aug 16	143		149	161	201
Aug 25	145		149	164	204
Sep 15	149		151	169	210

Oxygen ppm

Date	0	2	6	15
1948 Jul 5	6.2	6.2	1.3	0.1
Jul 12	6.6	7.4	1.1	0
Jul 19	6.7	6.7	1.7	0
Jul 26	6.6	6.8	1.7	0
Aug 2	6.5	6.5	1.3	0
Aug 9	6.7	6.8	1.2	0
1950 Jul 20	7.8	7.4	4.3	0
Aug 8	6.9	6.8	4.6	0
1951 Jul 20	6.1	4.2	2.9	0
Aug 16	6.4	4.9	2.4	0
Aug 25	6.8	5.2	2.0	0
Sep 15	6.9	5.8	1.6	0

Thermoclines enclosed in brackets

spring and fall overturns of 1951 as did the phosphorus fractions previously discussed.

The most constant fraction of phosphorus, during the period of investigation, that is from a quantitative point of view, was the soluble organic phosphorus. In only three samples, of all those collected at all the depths and throughout the entire length of the investigation, did the soluble organic phosphorus exceed 9 micrograms per liter (table 4). The majority of samples contained it in amounts ranging between 0 and 9 micrograms per liter. With regard to the previously mentioned three samples, the first was collected on July 25, 1950, at 20 meters and contained 12 micrograms per liter. The second was collected at the surface on August 14, 1950, and contained 11 micrograms per liter whereas the third was collected at 20 meters on September 16, 1950, and contained 22 micrograms per liter. The latter amount occurred in the same sample that contained large amounts of the other phosphorus fractions and it should be remembered that this sample was collected a very short time before the fall overturn of 1950.

LANCASTER LAKE

For a lake with such a small surface area, this one has considerable depth in addition to a steeply sloping floor. These features together with the protection and shelter it receives from the surrounding hills and forests, make for a very marked thermal stratification. This is well demonstrated in table 5 which presents data on water temperatures collected during the three summers of 1948, 1950 and 1951. Considering the data from the three summers as a whole, it can be seen that on the average, the epilimnion occupies the upper 2 meters of the 17-meter depth. The thermocline in general takes up the next three meters with a temperature difference of approximately 12 degrees centigrade between the upper and lower limits of this stratum. The hypolimnion, therefore, occupies the remaining depth of the lake which amounts to a stratum 12 meters thick. The surface temperatures during each of the summers were always very close to the air temperatures, deviating from it by only two or three degrees. The bottom temperatures always varied between 4.7 and 5.8° C.

The water of this lake is highly colored. Eggleton (1935) recorded the brown color as 59 units on the platinum-cobalt standard scale using the standard comparator of the United States Geological Survey.

Chemical stratification was also very marked in this lake. Carbonates fluctuated between 0 and 14 ppm in the epilimnion, and, in general, the difference in amounts present in the upper and lower limits of this stratum never exceeded 4 ppm. The hypolimnion contained no trace of carbonates The bicarbonate content of the epilimnion ranged between 120 and 153 ppm. The difference between the upper and lower limits never exceeded 5 ppm, and more often was less. At the bottom of the hypolimnion, the bicarbonate content of the waters varied between 180 and 210 ppm, occurring at the lower end of the range in the beginning of the summer and increasing gradually as the summer progressed. Determinations in a single vertical series of samples indicated a gradual increase of bicarbonates toward the bottom of the lake. The pH ranged between 8.0 and 8.2 in the epilimnion and between

TABLE 6.—Phosphorus data from Lancaster Lake during the summers of 1950-1951. Values of the total and the various fractions of phosphorus are reported in the body of the table as micrograms per liter.

| | | Total Phosphorus | | | | | | | | |
| | | Depth in meters | | | | | | | | |
		0	3	6	9	12	13	14	15	15.5
1950	Jul. 20	8	10	5	....	....	....	....	39	....
	Aug. 8	8	7	8	....	....	....	....	62	....
1951	Jul. 20	9	11	10	....	9	15	23	43	67
	Aug. 16	8	10	9	....	12	25	42	136	199
	Aug. 25	6	6	6	10	12	23	76	102	150
	Sep. 15	11	10	9	11	12	52	95	110	131

| | | Soluble inorganic Phosphorus | | | | | | | | |
| | | Depth in meters | | | | | | | | |
		0	3	6	9	12	13	14	15	15.5
1950	Jul. 20	1	2	2	....	....	....	....	23	....
	Aug. 8	2	2	3	....	....	....	....	41	....
1951	Jul. 20	1	1	2	....	3	7	13	30	49
	Aug. 16	1	1	1	....	5	15	30	120	175
	Aug. 25	0	0	1	3	6	14	65	85	130
	Sep. 15	3	2	2	3	6	42	83	95	110

| | | Total organic Phosphorus | | | | | | | | |
| | | Depth in meters | | | | | | | | |
		0	3	6	9	12	13	14	15	15.5
1950	Jul. 20	7	8	3	....	....	....	....	16	....
	Aug. 8	6	5	5	....	....	....	....	21	....
1951	Jul. 20	8	10	8	....	6	8	10	13	18
	Aug. 16	7	9	8	....	7	10	12	16	24
	Aug. 25	6	6	5	7	6	9	11	17	20
	Sep. 15	8	8	7	8	6	10	12	15	21

| | | Sestonic Phosphorus | | | | | | | | |
| | | Depth in meters | | | | | | | | |
		0	3	6	9	12	13	14	15	15.5
1950	Jul. 20	2	3	2	....	....	....	....	5	....
	Aug. 8	2	1	3	....	....	....	....	6	....
1951	Jul. 20	2	3	3	....	2	3	4	4	10
	Aug. 16	2	3	2	....	3	4	4	5	11
	Aug. 25	2	1	2	2	2	3	3	6	10
	Sep. 15	2	2	3	3	4	4	6	8	11

| | | Soluble organic Phosphorus | | | | | | | | |
| | | Depth in meters | | | | | | | | |
		0	3	6	9	12	13	14	15	15.5
1950	Jul. 20	5	5	1	....	....	....	....	11	....
	Aug. 8	4	4	2	....	....	....	....	16	....
1951	Jul. 20	6	7	5	....	4	5	6	9	8
	Aug. 16	5	6	6	....	4	6	8	11	13
	Aug. 25	4	5	3	5	4	6	8	11	10
	Sep. 15	6	6	4	5	2	6	6	7	10

7.1 and 7.3 at the bottom of the hypolimnion. Dissolved oxygen occurred in the epilimnion in amounts ranging between 7.8 and 8.2 ppm. In the hypolimnion it gradually decreased from top to bottom, usually disappearing from the bottom very early in the summer. There was no trace of dissolved carbon dioxide in the epilimnion on any day during the three summers. The upper limit of the hypolimnion, however, contained it in amounts varying between 7 and 13 ppm and in the lower limits it was present in amounts ranging between 10 and 19 ppm. The bottom waters of the hypolimnion always contained more than the upper waters of this stratum but the difference between the amounts of carbon dioxide in its upper and lower limits never exceeded 6 ppm. The conductivity of the water at the time of thermal stratification increased from surface to bottom. The values obtained showed, on the average, an increase from 240 mhos at the surface to 350 mhos at the bottom.

The total phosphorus in the epilimnion during both summers in which these determinations were made (table 6), occurred in amounts between 6 and 11 micrograms per liter. In the hypolimnion, the amounts increased toward the bottom, and at the bottom there was an appreciable increase as

TABLE 7.—A comparison of the soluble inorganic phosphorus in Douglas and Lancaster lakes during the summer of 1951. (Values of the total and the various fractions of phosphorus are reported in the body of the table as micrograms per liter).

Lakes		Depth in meters								
		0	2	3	5	6	9	12	13	14
Douglas	Jul. 9	1	2	....	1	....	....	2	....	....
	Jul. 23	1	1	....	1	....	....	1	....	....
	Aug. 10	1	1	....	1	....	....	1	....	....
	Aug. 25	1	1	....	1	....	....	1	....	....
	Sep. 15	1	1	....	1	....	....	1	....	....
	Oct. 6	2	2	....	1	....	....	1	....	....
Lancaster	Jul. 20	1	....	1	....	2	....	3	7	13
	Aug. 16	1	....	1	....	1	....	5	15	30
	Aug. 25	0	....	0	....	1	3	6	14	65
	Sep. 15	3	....	2	....	2	3	6	42	83

Lakes		Depth in meters							
		15	15.5*	16	17	18	19	20	20.5*
Douglas	Jul. 9	....	....	....	....	....	....	2	4
	Jul. 23	....	....	....	....	....	....	3	6
	Aug. 10	....	....	1	....	1	1	4	15
	Aug. 25	....	....	1	1	1	1	2	85
	Sep. 15	....	....	1	1	3	7	20	80
	Oct. 6	....	....	1	....	1	1	2	8
Lancaster	Jul. 20	30	49	....	....	....	....	....	....
	Aug. 16	120	175	....	....	....	....	....	....
	Aug. 25	85	130	....	....	....	....	....	....
	Sep. 15	95	110	....	....	....	....	....	....

* Water samples taken at these bottom depths were muddy. These samples were collected with a Kemmerer sampler and transferred to 250 cc. bottles. Each bottle was allowed to stand for two or three hours until the mud settled to the bottom. The clear water in the upper part of the bottle was analyzed.
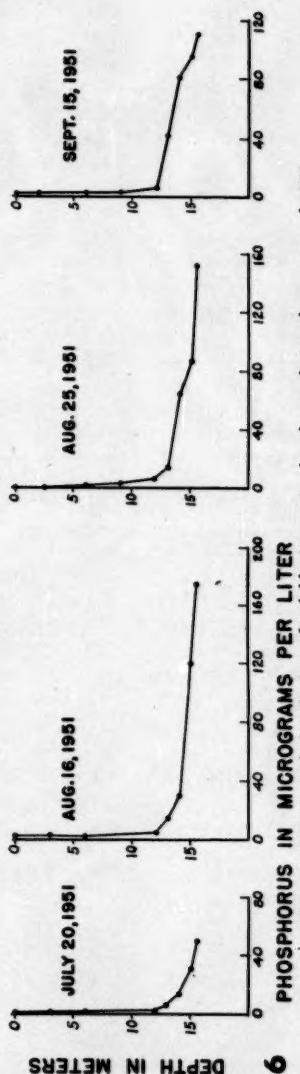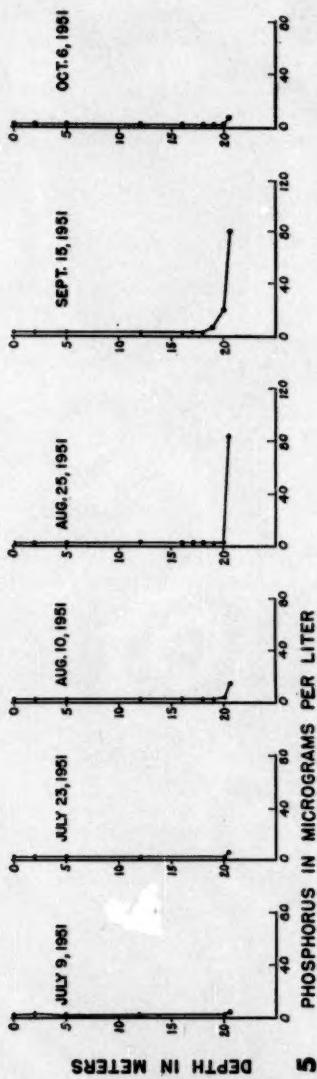
Figs. 5, 6.—Vertical distribution of soluble inorganic phosphorus during the summer of 1951.
5. Douglas Lake (South Fishtail Bay); 6. Lancaster Lake.

the summer progressed. In the summer of 1951 on July 20, the amount present at the bottom was 67 micrograms per liter. By August 16 it had increased to 199 micrograms per liter. This was the highest value obtained during the summer of that year. From then on, even before the fall overturn

occurred, the amount began to decrease, reaching 150 micrograms per liter by August 25 and 131 micrograms per liter by September 15. No determinations were made during the overturn.

In the epilimnion, the soluble inorganic phosphorus was present in very small amounts, fluctuating between 0 and 3 micrograms per liter. In the hypolimnion, its trend of distribution was very similar to that of total phosphorus. There was a gradual increase toward the bottom and, as was the case with the total phosphorus in the summer of 1951, there was also an increase of soluble inorganic phosphorus in the bottom waters as the summer progressed. Here too, however, the amounts began to decrease before the inception of the fall overturn. This trend can best be illustrated by stating the amounts of soluble inorganic phosphorus in the bottom waters on various successive dates during the summer. These values were 49, 175, 130 and 110 micrograms per liter. The amount present at the bottom on September 15, the last day of collection, was still high compared to the amount present in the early summer.

The vertical distribution of soluble inorganic phosphorus in Lancaster Lake during the summer of 1951 is demonstrated in table 7 and fig. 6. The increases that occurred at the bottom during the summer have been discussed but it can be seen how slowly it diffuses upward into the hypolimnion. By September 15 it had diffused up to 13 meters, a distance of only 2.5 meters. The upper limit of the hypolimnion on that day was between 4 and 5 meters.

The amount of total organic phosphorus in the epilimnion fluctuated between 6 and 8 micrograms per liter during both summers. It decreased in amount toward the bottom of the hypolimnion. At the extreme bottom, the total organic phosphorus varied between 18 and 24 micrograms per liter.

The sestonic phosphorus was present in amounts which nearly always ranged between 1 and 6 micrograms per liter at all depths except at the 15.5-meter depth. Here it fluctuated between 10 and 11 micrograms per liter. The tendency seemed to be a very gradual increase from top to bottom.

The values of soluble organic phosphorus obtained from water samples collected through the summers at various depths in the upper 14 meters ranged between 4 and 8 micrograms per liter in the majority of samples. At the bottom depth it occurred in amounts ranging between 10 and 16 micrograms per liter in most cases. Those samples which contained soluble organic phosphorus in amounts outside of the ranges mentioned were few and their deviations small.

MUNRO LAKE

This lake is shallow and relatively unprotected, hence its waters are in constant circulation during the absence of an ice cover. Most of the physico-chemical data collected during the summers of 1948, 1950 and 1951 (table 8) demonstrate a uniformity of conditions from top to bottom at any single time of sampling. Considering the data from the three summers as a whole, it can be seen that the water temperatures always ranged between 18.4 and 27.4° C. The differences between the surface and bottom temperatures at any one time never exceeded more than one degree. The carbonates occurred in amounts ranging between 4 and 12 ppm, whereas the bicarbonates were

TABLE 8.—Physico-chemical data from Munro Lake during the summers of 1948-'50-'51.

			Water Temperatures in degrees Centigrade		Carbonates ppm		Bicarbonates ppm	
			Depth in meters					
			0	2	0	2	0	2
1948	Jul.	3	20.0	19.6	4	8	94	90
	Jul.	10	27.4	26.4	12	8	90	96
	Jul.	24	18.5	18.4	8	12	82	74
	Jul.	31	21.0	21.0	6	8	87	86
	Aug.	12	20.8	20.4	6	6	90	92
1950	Jul.	27	22.5	22.2	4	4	108	112
	Aug.	15	22.8	22.8	6	6	110	112
1951	Jul.	18	22.8	22.6	6	6	97	97
	Aug.	15	20.6	20.4	5	5	107	107

			pH		Oxygen ppm		Carbon dioxide ppm	
			Depth in meters					
			0	2	0	2	0	2
1948	Jul.	3	8.2	8.0	8.2	8.0	0	0
	Jul.	10	8.3	8.3	7.2	7.1	0	0
	Jul.	24	8.2	8.1	8.1	8.0	0	0
	Jul.	31	8.4	8.4	7.1	7.2	0	0
	Aug.	12	8.3	8.3	6.8	6.8	0	0
1950	Jul.	27	8.3	8.3	7.4	7.2	0	0
	Aug.	15	8.2	8.2	7.1	7.0	0	0
1951	Jul.	18	8.3	8.3	8.7	8.6	0	0
	Aug.	15	8.3	8.3	8.1	8.0	0	0

present in quantities varying between 74 and 112 ppm. The pH was always between 8.0 and 8.3 during the three summers, never differing from surface to bottom by more than 0.2. Dissolved oxygen in this lake was present in amounts ranging from 6.2 to 8.7 ppm. Here, again, the difference between the quantities in the surface and bottom waters on a single day was only a fraction of a part per million. No trace of dissolved carbon dioxide was found in any of the water samples collected. Welch (1938a) reported the color of the water in this lake to be usually less than 20 on the platinum cobalt scale. Conductivity measurements from this lake showed variations between 180 and 200 mhos.

The amounts of total phosphorus (table 9) in Munro Lake during the two summers in which these determinations were made fluctuated between 10 and 12 micrograms per liter whereas the soluble inorganic phosphorus occurred in amounts between 1 and 2 micrograms per liter. The total organic phosphorus was present in quantities ranging between 9 and 11 micrograms per liter. Determinations of sestonic phosphorus indicate its presence in amounts varying between 2 and 5 micrograms per liter while the soluble organic phosphorus occurred in quantities ranging between 5 and 8 micrograms per liter. It will thus be seen that, in terms of total phosphorus, Munro Lake is quite similar to the epilimnion of Lancaster and Douglas Lakes.

TABLE 9.—Phosphorus data from Munro Lake during the summers of 1950-1951. (Values of the total and the various fractions of phosphorus are reported in the body of the table as micrograms per liter).

			Phosphorus								
		Total		Soluble Inorganic		Total Organic		Sestonic		Soluble Organic	
						Depth in meters					
		0	2	0	2	0	2	0	2	0	2
1950	Jul. 27	10	12	1	1	9	11	2	3	7	8
	Aug. 15	12	11	2	1	10	10	4	5	6	5
1951	Jul. 18	11	10	1	1	10	9	3	4	7	5
	Aug. 15	12	12	1	1	11	11	3	4	8	7

VINCENT LAKE

This lake is also shallow, hence thermal stratification does not ordinarily persist throughout a whole summer. Due to much flocculent material in the lower levels, the lake is quite turbid. Welch (1938) states that in times of calm, however, the surface water is quite transparent and the color low, varying

TABLE 10.—Physico-chemical data from Vincent Lake during the summers of 1948-'50-'51.

		Water Temperatures in degrees Centigrade		Carbonates ppm		Bicarbonates ppm	
				Depth in meters			
		0	2.5	0	2.5	0	2.5
1948	Jul. 3	21.1	20.6	0	0	6	7
	Jul. 10	27.1	23.8	0	0	4	5
	Jul. 24	22.4	22.0	0	0	4	4
	Jul. 31	24.0	23.2	0	0	5	5
	Aug. 12	22.1	21.8	0	0	5	5
1950	Jul. 28	24.0	21.8	0	0	7	7
	Aug. 17	23.0	22.6	0	0	8	9
1951	Jul. 18	23.1	22.9	0	0	7	7
	Aug. 15	20.3	20.0	0	0	8	9

		pH		Oxygen ppm		Carbon dioxide ppm	
				Depth in meters			
		0	2.5	0	2.5	0	2.5
1948	Jul. 3	6.6	6.6	7.3	7.1	1	1
	Jul. 10	7.5	7.4	6.9	6.4	1	1
	Jul. 24	7.2	7.2	7.6	7.7	1	1
	Jul. 31	7.0	6.8	7.6	7.4	1	1.5
	Aug. 12	7.1	7.0	7.5	7.4	1	1
1950	Jul. 28	7.3	6.4	7.2	6.3	0.3	1.2
	Aug. 17	7.1	6.6	7.4	7.0	0.3	1.0
1951	Jul. 18	7.2	7.0	7.0	6.9	0.5	1.0
	Aug. 15	7.3	6.8	7.5	7.0	0.8	1.2

TABLE 11.—Phosphorus data from Vincent Lake during the summers of 1950-1951.
(Values of the total and the various fractions of phosphorus are reported
in the body of the table as micrograms per liter).

					Phosphorus					
		Total		Soluble Inorganic		Total Organic		Sestonic		Soluble Organic
						Depth in meters				
		0	2.5	0	2.5	0	2.5	0	2.5	0	2.5
1950 Jul. 28		16	18	0.5	0	15.5	18	4.5	3	11	15
Aug. 17		16	15	0.0	1	16	14	10	9	6	5
1951 Jul. 18		14	16	1.0	1	13	15	9	10	4	5
Aug. 15		17	17	1.0	1	16	16	8	9	8	7

from about 27 to 31 on the platinum cobalt scale. Physico-chemical conditions
were usually uniform from surface to bottom on any one day when deter-
mined during this investigation (table 10). During the three summers of
investigation the water temperatures fluctuated between 20.0 and 27.1 degrees
centigrade. There was no trace of carbonates at any time, and the bicarbonate
content of the water varied between 4 and 9 ppm which was much less than
was present in the other lakes under investigation. The pH values obtained
for this lake during the present investigation are interesting when compared
to those values obtained by other workers in previous years. Jewell and
Brown (1929) reported the pH as varying between 4.4 and 7.2 during the
years 1923 and 1926. Eggleton (1935) found the pH to vary between 5.7
and 7.0 for the years 1926 and 1933. The present writer obtained values
between 6.4 and 7.5 for the years 1948 and 1951 but in only one-third of
the samples collected was the pH below 7. Considering the data of the three
writers, it appears that a gradual change is taking place in Vincent Lake from
an acid to an alkaline condition. Dissolved oxygen occurred in abundance
varying in amounts from 6.3 to 7.6 ppm. Dissolved carbon dioxide on the
other hand occurred in small amounts ranging between 0.3 and 1.5 ppm.
Conductivity readings from this lake varied between 18 and 25 mhos, which
is very low compared to the other lakes.

Determinations of total phosphorus (table 11) showed its presence in
quantities varying from 14 to 18 micrograms per liter. Soluble inorganic
phosphorus occurred in minimal quantities ranging between 0 and 1 micro-
grams per liter. The total organic phosphorus varied in amounts from
13 to 18 micrograms per liter. Analysis of the sestonic phosphorus showed
that it occurred in amounts ranging from 3 to 10 micrograms per liter and
the soluble organic phosphorus was present in quantities varying from 4 to
15 micrograms per liter. It thus is evident that the total organic phosphorus
is higher than in any of the other three lakes previously discussed.

LAKE LANSING

Work was conducted on this lake from August 28 through November
9, 1950. On August 28 there was evidence of a slight thermal stratification
(table 12), the thermocline occurring between 4 and 5 meters and having a
temperature difference of only $1.1°$ C. between its upper and lower limits.

TABLE 12.—Physico-chemical data from Lake Lansing during fall of 1950.

	Water temperatures in °C.					Oxygen ppm			
	Depth in meters								
	0	2	4	5	9	0	2	5	9
Aug. 28	23.3	22.2	[21.1	20.0]	18.9	7.9	7.5	5.0	0.0
Sep. 4	20.6	20.6	20.6	20.6	19.4	6.1	6.1	6.1	0.2
Sep. 16	18.9	18.9	18.9	18.9	18.4	6.2	6.2	6.3	5.7
Oct. 3	18.3	....	....	....	16.6	8.4	8.0	6.4	4.7
Oct. 24	11.6	....	....	....	11.6	7.6	....	....	5.2
Nov. 9	10.0	....	....	....	10.0	6.8	....	....	6.2

	pH				Carbonates ppm			
	Depth in meters							
	0	2	5	9	0	2	5	9
Aug. 28	8.4	8.4	7.9	7.4	8	10	0	0
Sep. 4	8.0	8.0	8.0	7.4	0	0	0	0
Sep. 16	7.7	7.7	7.7	7.7	0	0	0	0
Oct. 3	8.1	....	....	7.4	0	0	0	0
Oct. 24	7.9	....	....	7.9	0	0	0	0
Nov. 9	7.9	....	....	7.8	0	0	0	0

	Bicarbonates ppm				Carbon dioxide ppm			
	Depth in meters							
	0	2	5	9	0	2	5	9
Aug. 28	98	95	106	112	0.0	0.0	0.6	4.8
Sep. 4	104	105	105	116	0.0	0.0	0.0	0.5
Sep. 16	108	108	107	108	0.8	0.8	0.8	0.8
Oct. 3	115	115	115	114	0.0	....	....	12.0
Oct. 24	117	117	116	114	0.3	....	....	0.3
Nov. 9	114	114	114	115	0.3	....	....	0.4

Thermoclines enclosed in brackets.

During the remainder of the period of investigation there were, sometimes, slight decreases in temperature from top to bottom but they were not sufficiently great to form a thermocline which would fit the classical definition of a one-degree centigrade drop per meter of depth. On August 28 and September 4 there was an abundance of dissolved oxygen at all depths, except at the bottom (fig. 7). At the latter depth, there was no oxygen on the first day and only 0.2 ppm on the second. By September 16, circulation was in progress and there was oxygen present at all depths during the remainder of the fall, in amounts varying between 4.7 and 8.4 ppm. On August 28, all through the epilimnion, the pH was 8.4 while in the hypolimnion it was 7.9 and 7.4 at its upper and lower limits respectively. During the remainder of the investigation the pH fluctuated between 7.7 and 8.1 at the surface and between 7.4 and 7.9 at the bottom. On the first day of collection carbonates occurred only in the upper two meters and in amounts between 8 and 10 ppm. On the other days of collection there was no trace of carbonates at any depth. The bicarbonate content on August 28 occurred in amounts between 95 and 98 ppm in the epilimnion and between 106 and 112 ppm in the hypolimnion. On September 4, approximately one week later, there were between 104 and
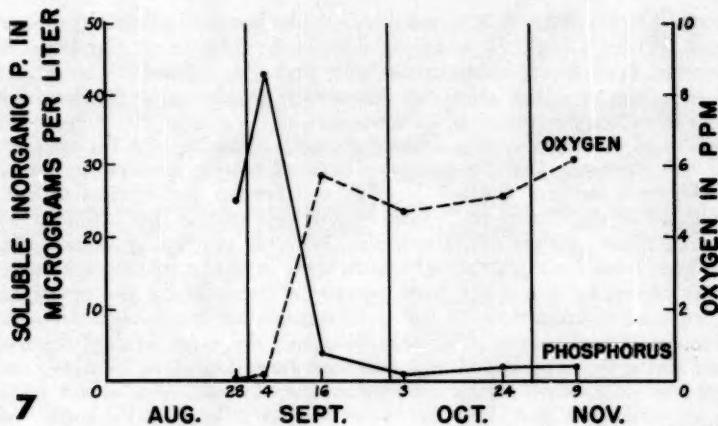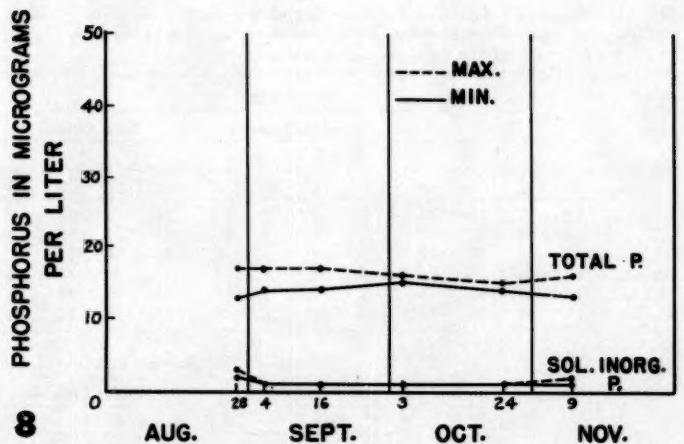
Figs. 7, 8.—7. Soluble inorganic phosphorus and dissolved oxygen in Lake Lansing at 8-meter depth (bottom), during fall of 1950. 8. Maximum and minimum values of total phosphorus and soluble inorganic phosphorus occurring between surface and 5-meter depth in Lake Lansing during fall of 1950.

105 ppm of bicarbonates at all the depths except the bottom which contained 116 ppm. During the remainder of the period of investigation the bicarbonate content in the surface varied between 108 and 117 ppm whereas at the bottom it fluctuated between 108 and 115 ppm; the difference between the amounts in the surface and bottom never exceeding 3 ppm. On August 28 there was no trace of dissolved carbon dioxide in the upper two meters, but from the 5-meter to the 9-meter depth it appeared in increasing amounts from 0.6 to 4.8

ppm. On September 4, it occurred only at the bottom depth in the amount of 0.5 ppm. On all the remaining days in the field, except October 3, it occurred at all depths in amounts ranging from 0 to 0.8 ppm. On October 3 there was no carbon dioxide in the surface sample but at the bottom it was present in the amount of 12 ppm.

All of the water samples collected from Lake Lansing with the exception of two, contained total phosphorus in amounts ranging between 13 and 17 micrograms per liter (table 13). The two samples just referred to were collected at the bottom on August 28 and September 4 and contained 33 and 57 micrograms per liter respectively. With the exception of the same two samples, soluble inorganic phosphorus occurred in all the collections in quantities varying between 1 and 3 micrograms per liter. In the two exceptions, it occurred in amounts of 25 and 43 micrograms per liter respectively. The amounts of total organic phosphorus throughout the entire depth of the lake and during the whole period of investigation varied from 8 to 16 micrograms per liter. The soluble organic phosphorus occurred in quantities between 1 and 8 micrograms per liter except in the two samples collected at the bottom on

TABLE 13.—Phosphorus data from Lake Lansing during the fall of 1950. (Values of the total and various fractions of phosphorus are reported in the body of the table as micrograms per liter).

		Phosphorus										
		Total				Soluble Inorganic				Total Organic			
		Depth in meters											
		0	2	5	9	0	2	5	9	0	2	5	9
Aug. 28		14	17	13	33	3	2	2	25	11	15	11	8
Sep. 4		16	14	17	57	1	1	1	43	15	13	16	14
Sep. 16		14	17	15	15	1	1	1	4	13	16	14	11
Oct. 3		15	16	16	15	1	1	1	1	14	15	15	14
Oct. 24		14	14	15	15	1	1	1	2	13	13	14	13
Nov. 9		16	14	13	14	1	2	1	2	15	12	12	12

	Phosphorus							
	Sestonic				Soluble Organic			
	Depth in meters							
	0	2	5	9	0	2	5	9
Aug. 28	10	13	7	23*	1	2	4	0
Sep. 4	11	9	12	27**	4	4	4	0
Sep. 16	7	12	9	9	6	4	5	2
Oct. 3	7	9	8	9	7	6	7	5
Oct. 24	6	7	8	8	7	6	6	5
Nov. 9	7	8	6	7	8	4	6	5

* On Aug. 28, the 23 micrograms of sestonic phosphorus at 9 meters included 15 micrograms of acid soluble sestonic phosphorus leaving 8 micrograms of actual organic sestonic phosphorus.

** On Sept. 4, the 27 micrograms of sestonic phosphorus at 9 meters included 13 micrograms of acid soluble sestonic phosphorus leaving 14 micrograms of actual organic sestonic phosphorus.

August 28 and September 4. In the latter samples no soluble organic phosphorus was found. All of the samples with the exception of the two bottom ones previously mentioned, contained sestonic phosphorus in amounts ranging between 7 and 13 micrograms per liter. The exceptions contained it in amounts of 23 and 27 micrograms per liter respectively. It should be remembered that these two bottom water samples collected singly on August 28 and September 4 were the ones which contained no oxygen or just a trace thereof.

A quantitative and qualitative analysis of the seasonal and vertical distribution of phytoplankton in these lakes and the relation of phytoplankton periodicity to the physicochemical nature of the environment is discussed in Part II of this paper (pp. 334-370).

The Relation of Phytoplankton Periodicity to the Nature of the Physico-Chemical Environment With Special Reference to Phosphorus[1,2]

II. Seasonal and Vertical Distribution of the Phytoplankton in Relation to the Environment.

Allan Tucker

Michigan State University, East Lansing

This investigation was undertaken in an attempt to discover relationships which may exist between the abundance and periodicity of phytoplankton, and the physico-chemical environment. Plankton samples and physico-chemical data were collected from Douglas Lake in northern Michigan during the summer of 1948 and during 16 consecutive months from July 3, 1950 to October 6, 1951. In addition, similar data were collected during the summers of 1948, 1950 and 1951 from Munro, Vincent and Lancaster lakes in northern Michigan and during the fall of 1950 from Lake Lansing in southern Michigan. Part I deals with the morphometrical, physical and chemical conditions of the lakes investigated (Tucker, 1957). This paper, Part II, consists of a qualitative and quantitative analysis of the seasonal and vertical distribution of phytoplankton of these lakes and a discussion of the relation of phytoplankton periodicity to the environment.

Methods of Collection and Enumeration

Collection.—A single station was chosen in each of the lakes, from which to take vertical series of plankton samples. The apparatus employed to collect these samples was a Birge and Juday 10 liter trap with number 25 silk bolting cloth. The samples were concentrated to approximately 15 or 20 ml, depending upon the concentration of plankton in the lake at the time, and transferred to one ounce packer bottles. About eight drops of formalin were added to each bottle as a preservative.

Enumeration.—Enumeration of phytoplankton was done in general as outlined in Whipple (1927). A binocular compound microscope was used with 16 mm objectives and 10X oculars. In the right ocular was placed a Whipple ocular micrometer calibrated to include a one mm square field. The counting chamber was a Sedgewick-Rafter cell.

TABLE 14.—Species of phytoplankton making up the genera which have quantitative significance in the plankton samples collected from Douglas, Lancaster, Munro, Vincent, and Lansing lakes.

Phytoplankton	Douglas	Lancaster	Munro	Vincent	Lansing
BLUE-GREEN ALGAE					
Anabaena flos-aquae (Lyngb.) Breb.	X	X			X
A. sp.			X		X
Aphanizomenon flos-aquae (S.) Ralfs			X		
Chroococcus giganteus W. West			X		
C. limneticus Lemm.			X	X	
C. minor (Kuetz.) Nag.				X	
C. sp.		X			
Coelosphaerium kuetzingianum Nag.	X				
C. sp.		X		X	X
Merismopedia punctata Meyen	X				
M. sp.			X	X	X
Microcystis aeruginosa Kuetz.	X		X	X	X
M. flos-aquae (Wittrock) Kirchner			X	X	
M. ichthyoblabe Kuetz.	X		X		
M. incerta Lemm.	X				X
M. sp.		X		X	
Oscillatoria tenuis Ag.	X				
O. sp.	X				X
GREEN ALGAE					
Arthrodesmus sublatus Kuetz.				X	
A. Ralfsii W. West				X	
A. sp.	X	X			
Cosmarium sp.	X	X			X
Dictyosphaerium pulchellum Wood					X
Eudorina elegans Ehr.		X	X		X
Pediastrum Boryanum (Turp.) Menegh.	X	X	X		
P. duplex Meyen	X		X	X	X
P. sp.	X				X
P. tetras (Ehr.) Ralfs			X		
Scenedesmus armatus (Chod.) G. M. Smith	X				
S. acuminatus (Lagerh.) Chod.	X				
S. quadricauda (Turp.) Breb.	X				
S. bijuga (Turpin) Lag.	X		X	X	
Staurastrum arctiscon (Ehr.) Lundell			X	X	
S. Brachiatum Ralfs			X		
S. leptocladum v. sinuatum G. M. Smith	X				
S. cuspidatum Breb.				X	
S. paradoxum Meyen	X		X	X	
S. polymorphum Breb.	X				
S. sp.					X
S. arachne Ralfs				X	
S. O'Mearii minutum W. West				X	
Tetraedron sp.					X
Xanthidium antilopaeum (Breb.) Kuetz.				X	

TABLE 14 (*Continued*)

Phytoplankton	Douglas	Lancaster	Munro	Vincent	Lansing
DIATOMS					
Asterionella formosa Hass.	X	X	X		X
Fragilaria crotonensis Kitt.	X	X	X		X
F. sp.					X
Melosira granulata (Ehr.) Ralfs	X				
M. varians Ag.	X			X	X
M. sp.		X	X		
Navicula sp.	X	X	X	X	X
Stephanodiscus niagarae Ehr.	X	X			
S. sp.			X	X	X
Synedra acus Kuetz.	X				
S. pulchella v. longissima W. Smith	X				X
S. ulna (Nitzsh.) Ehr.	X				
S. sp.		X	X	X	
Tabellaria fenestrata Kuetz.	X			X	
T. flocculosa (Roth) Kuetz.	X			X	
T. sp.		X	X		
DINOFLAGELLATES					
Ceratium hirundinella (O.F.M.) Schrank	X	X	X		X
Peridinium cinctum Ehr.		X			
P. Westi Lemm.	X				
P. wisconsinense Eddy					
P. sp.		X	X	X	
CHRYSOPHYCEAE					
Dinobryon sertularia Ehr.	X	X			X
D. sociale Ehr.	X	X	X	X	X
D. divergens Imhof			X		X
Synura Uvella Ehr.		X			

The phytoplankton were counted by genera only as it was impossible to place the high power objective over the Sedgewick-Rafter cell. Some qualitative studies, however, were done and those genera which appeared in the samples in sufficiently large numbers to make them quantitatively significant were identified to species where possible (table 14), while those which occurred in very small numbers were ignored from the standpoint of species identification.

The actual enumeration of the phytoplankton in a single field under the microscope was done in such a way that one organism did not necessarily constitute one unit but to each genus was allotted a certain number of cells per unit or a certain number of micra per unit if it were a filamentous alga. This system was used to reduce inconsistencies in results arising from the

variations in size of different individuals of the same genus. The number of cells or micra allotted to a single unit of a genus was the same as that used by Chandler (1940) in his counts of Lake Erie phytoplankton and by the present writer in the analysis of the phytoplankton of the Bay of Quinte (Tucker, 1948). By using a common system of enumeration, the results obtained from different lakes by various workers may be compared if desired, without the cumbersome task of converting the results of these investigations into comparable units. The number of cells or the length of a filament considered to be a single unit is shown in the following list:

Diatoms

Asterionella	8 cells	Stephanodiscus	1 cell
Fragilaria	100 micra	Synedra	1 cell
Melosira	300 micra	Tabellaria	8 cells
Navicula	1 cell		

Blue Green Algae

Anabaena	300 micra	Merismopedia	4 cells
Aphanizomenon	300 micra	Microcystis	10,000 sq. micra
Chroococcus	4 cells	Oscillatoria	300 micra
Coelosphaerium	1 colony		

Green Algae

Arthrodesmus	1 cell	Scenedesmus	4 cells
Cosmarium	1 cell	Staurastrum	1 cell
Dictyosphaerium	4 cells	Tetraedron	1 colony
Eudorina	1 colony	Xanthidium	1 cell
Pediastrum	1 colony		

Chrysophyceae

| Dinobryon | 5 cells | Synura | 1 colony |

Dinophyceae

| Ceratium | 1 colony | Peridinium | 1 colony |

In estimating phytoplankton populations it has always been a difficult problem to know how many random fields should be counted under the microscope in order to assure reliable results. Many workers have published papers critically discussing plankton counting techniques and suggesting methods which they believed would give the most accurate estimates. The literature pertaining to plankton enumeration has been reviewed by Serfling (1949). Chandler (1940) and Tucker (1948), in their enumeration technique, filled the counting chamber twice from each sample and counted 10 random fields each time, making a total of 20 fields counted for each sample. Serfling (1949) believes that the number of fields counted should depend on the concentration of the samples. He states, "The distribution of plankton in the counting chamber may vary from the expected distribution of a Poisson function by varying amounts. The departure varies with the species, the concentration of plankton and also from one preparation to another." As a result of his calculations he proposed that sets of 10 fields be counted until a total of 62 units are observed. This criterion was used in the present investigation.

In most of the samples, the minimum requirement of 62 units could be
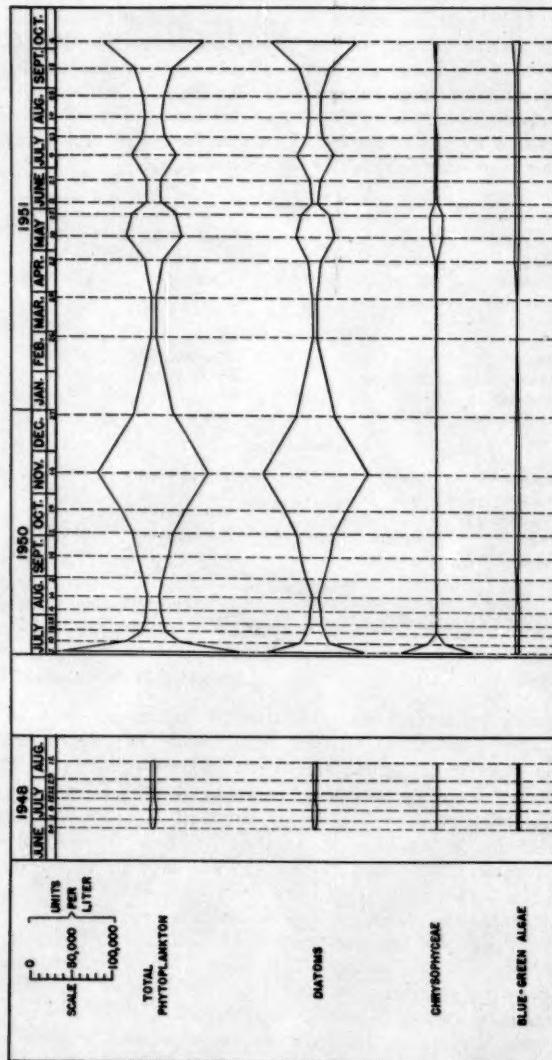
Fig. 9.—Seasonal variation in standing crops of total phytoplankton and the major classes of algae in Douglas Lake during the summer of 1948 and from July 3, 1950, to October 6, 1951. Fall overturn began between Sept. 16 and Oct. 2, 1950; ice appeared Nov. 24, 1950; ice disappeared April 13, 1951; thermal stratification began between May 10 and May 25, 1951; fall overturn began between Sept. 15, and Oct. 6, 1951.

fulfilled by counting 20 fields. In some cases 10 fields yielded the desired number of units and in others it was necessary to count 30 and occasionally 40 fields. A factor was calculated for each genus so that its quantity in units per liter could be determined. The standard crop of phytoplankton at a certain station on a given day was calculated by averaging the counts in the vertical series of samples collected on that day.

DOUGLAS LAKE

During that part of the summer of 1948 in which work was being carried on, the standing crop of total phytoplankton was very poor, ranging between 2,806 and 8,276 units per liter (fig. 9). If there had been a phytoplankton pulse, it must have occurred sometime before June 24. For the purpose of this investigation, a pulse has arbitrarily been defined as a standing crop containing at least 50,000 units per liter.

On July 3, 1950, the first day of the 16-month investigation, there was already in the Douglas Lake station, a pulse consisting of 219,352 units per liter (fig. 9). By July 10, this had decreased to 66,088 and on July 18 there were present only 29,954 units per liter. Evidently, the investigation had started just in time to witness the end of the spring pulse. The amount of total phytoplankton continued to decrease slightly until August 14 and from then on it began to increase; however, it never reached the status of a pulse until after October 2, which incidentally was a day not far past the beginning of the fall overturn. By that day the amount of phytoplankton had increased quite markedly, reaching its maximum, however, on November 14 when it was 136,440 units per liter. The days that followed saw a continual decrease which persisted under the ice and reached a low of 3,809 units per liter on February 26, 1951. There was not much of a quantitative change in the standing crop until after April 23. By this time the ice had disappeared and the lake was in the process of the spring overturn. On May 10, a pulse was present in the amount of 67,103 units per liter, however, it persisted only for two or three weeks and was followed by a decrease which was evidenced by the fact that on June 8 the standing crop was only 16,030 units per liter. In the two weeks that followed there was very little change but on July 9 another small pulse occurred (55,035 units per liter). This one persisted for an even shorter period of time than had its predecessor one month previously and on July 23 it was no longer present. From that day forward the standing crop did not increase sufficiently in amount to be called a pulse until sometime between September 15 and October 6. On the latter date, there were present 125,550 units per liter. This was probably the beginning of the fall pulse of 1951.

During the 16-month period of investigation, then, five separate pulses were observed. The first one was not observed in its entirety, but fortunately, plankton samples had been collected early enough in the season to observe the end of what must have been the spring pulse. The second pulse began almost immediately after the fall overturn of 1951 and may be called the fall pulse of that year. The spring pulse of 1951, for some reason, occurred in two shifts; the first of which commenced very soon after the spring overturn. The fall overturn of 1951 was followed very closely by the beginning
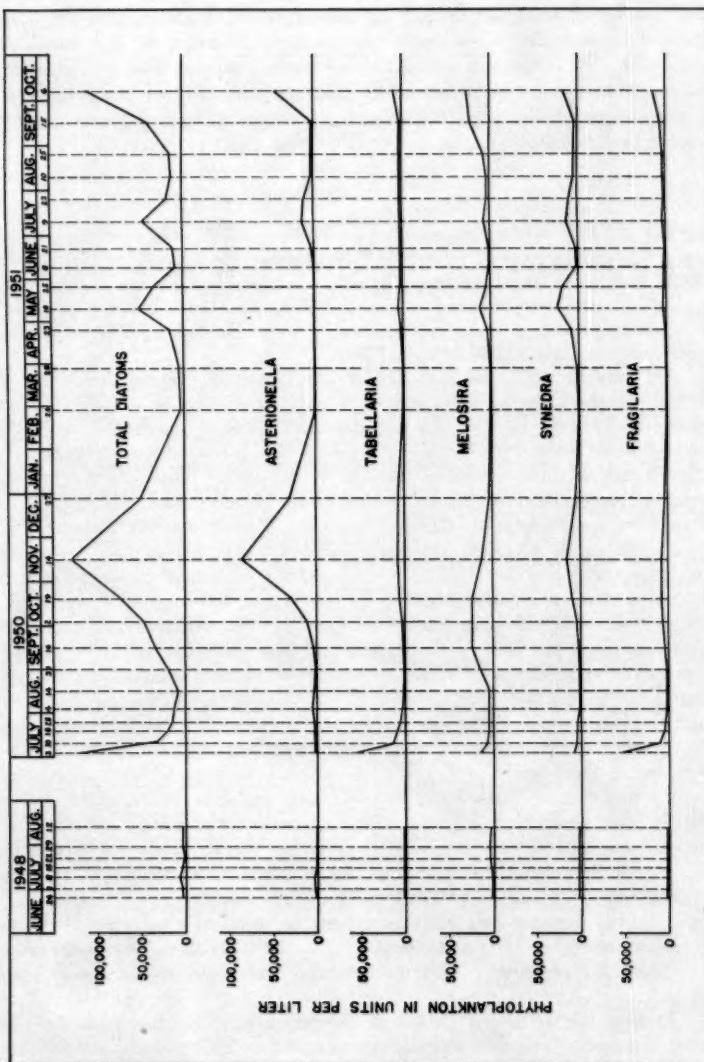
Fig. 10.—Seasonal variation in standing crops of total diatoms and the major genera of this class in Douglas Lake during the summer of 1948 and from July 3, 1950, to October 6, 1951. See explanation of fig. 9.

of the fall pulse, and since field work was terminated on October 6, 1951, the actual fate of this fall pulse was not observed.

Fig. 9 demonstrates without a doubt that Douglas Lake is a diatom lake. The average percentage of diatoms occurring in the standing crop of phytoplankton (considering the entire investigation as a whole) varied between 54.3 and 95.4 with a mean of 76.2 percent (fig. 12). The fall phytoplankton pulses of 1950 and 1951 each contained over 85 percent diatoms, the remainder of the crop being made up of the other four classes of algae. The genera which were most abundant amongst the diatoms in both of the fall pulses were *Asterionella, Melosira* and *Synedra* (fig. 10). The diatom population of the spring pulses in each of the two years made up only between 55 and 65 percent of the crop whereas the Chrysophyceae consisting wholly of *Dinobryon* contributed between 30 and 40 percent of the population. *Dinobryon* evidently shows up in significant numbers only in the spring. The genera making up the diatom population in the spring pulses were *Tabellaria, Melosira, Synedra* and *Fragilaria*. The genus *Asterionella* contributed to the spring pulse of 1951 but did not show up significantly in the plankton samples collected during the spring pulse of 1950. As was previously mentioned, the latter pulse was already in progress when the investigation was started and it could very well be that an *Asterionella*-peak had appeared and disappeared before the investigation was begun.

Blue-green algae occurred in all the samples and made up, on the average, about 10 percent of the crop, varying between 2.3 and 23.9 percent (fig. 12). They contributed very little to any pulse and for the most part were quite consistent quantitatively.

The green algae and Dinophyceae made up the remainder of the crop. Together they constituted an average of about 7 percent of the population. They, too, were consistent in their paucity and hence played no part in any of the pulses.

Fig. 11 shows the vertical distribution of total phytoplankton, diatoms and Chrysophyceae during the period of investigation. In general, it can be seen that each of the pulses first reached its maximum in the upper waters, but soon afterward, due to the stirring action in the water, the populations tended to be distributed almost uniformly from surface to bottom.

LANCASTER LAKE

In none of the three summers when samples were collected, did the standing crop reach a population equivalent to a pulse, that is an amount of at least 50,000 units per liter. Thermal stratification was very marked and the epilimion usually occupied only the upper three meters (Tucker, 1957). It can be seen (fig. 13) that, in the epilimnion, there was sufficient phytoplankton, at least on two occasions, July 20, 1950, and August 16, 1951, to warrant the population in this stratum being called a pulse. In spite of these minor pulses occurring in the epilimnion, it is probable, that, had a year-round study been made of the phytoplankton populations in Lancaster Lake, these summer crops would have appeared small in comparison to the yields which immediately follow the spring and fall overturns.

Five vertical series of plankton samples were collected at different times
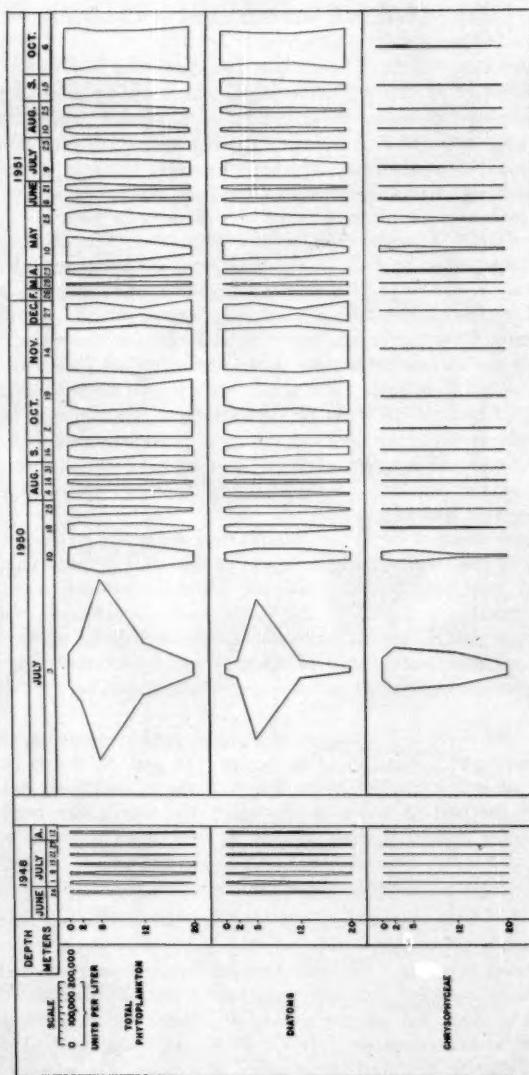
Fig. 11.—Vertical distribution of total phytoplankton and the major classes of algae in Douglas Lake during the summer of 1948 and from July 3, 1950 to October 6, 1951. See explanation of fig. 9.

during the summer of 1948, and the standing crop at each of these was calculated. The largest yield contained 7,610 and the smallest 2,538 units per liter. The Chrysophyceae, consisting mostly of *Synura*, made up between 58 and 86 percent in four of the crops and only 13 percent in the other. Diatoms
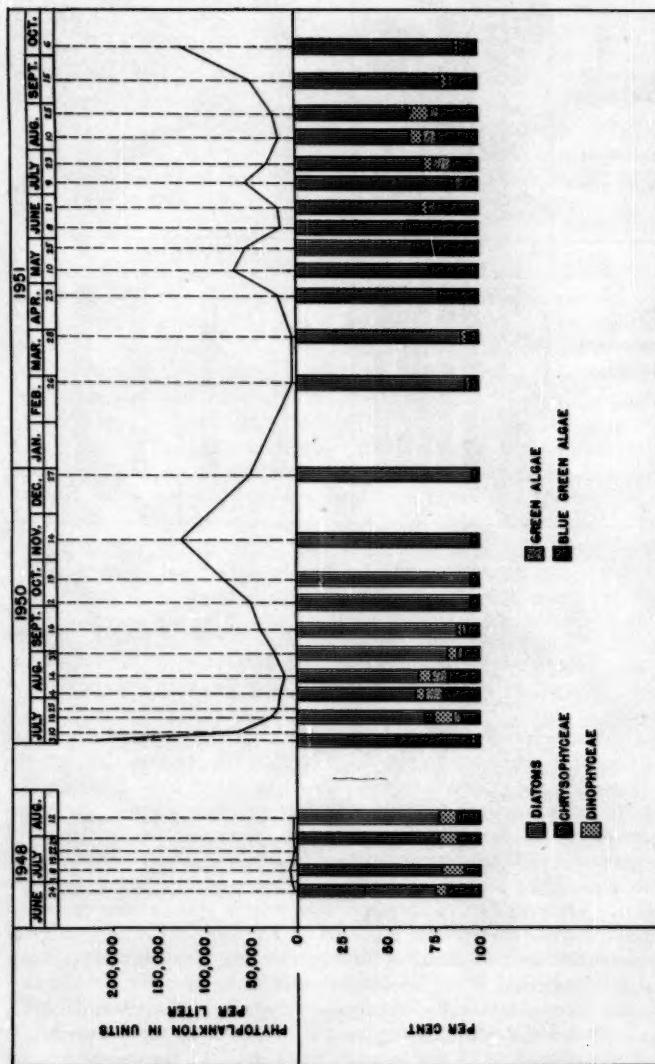
Fig. 12.—Seasonal variation in standing crops of total phytoplankton and their percentage composition in Douglas Lake during the summer of 1948 and from July 3, 1950, to October 6, 1951. See explanation of fig. 9.
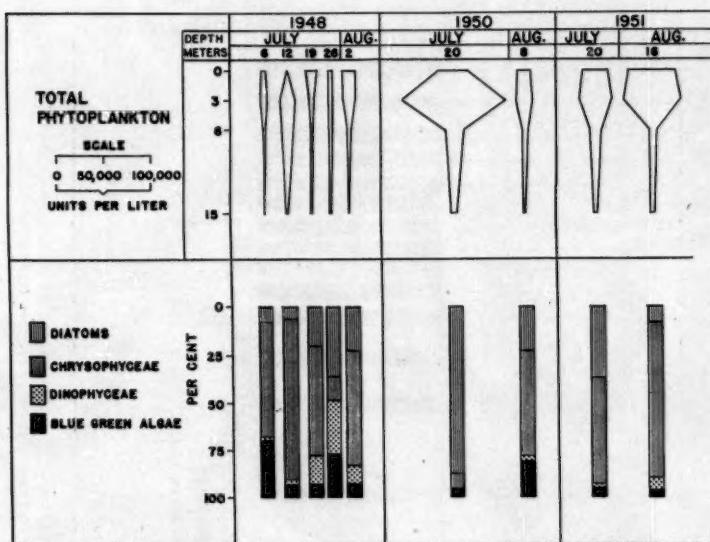
Fig. 13.—Vertical distribution and percentage composition of phytoplankton crops in Lancaster Lake during the summers of 1948, 1950 and 1951.

made up the next most abundant class averaging between 5 and 36 percent of the total. Dinophyceae and blue-greens together made up the remainder. Green algae occurred in very small numbers being less than one percent of the population.

During the summer of 1950, only two vertical series were collected, one on July 20 and the other on August 8. The standing crop on the first day was 42,791 and on the second day only 10,119 units per liter. On the first day (July 20), diatoms were the most abundant phytoplankters in the population contributing 88 percent. Chrysophyceae, again composed mainly of *Synura*, constituted 7.4 percent while the Dinophyceae and blue-greens, together with a negligible number of green algae, made up the remainder. On the second day (August 8) the Chrysophyceae were in the majority contributing 56.1 percent while the diatoms made up 23.5 percent. The remainder of the phytoplankton was composed of blue-greens and Dinophyceae. Again the green algae appeared in negligible quantities.

Two vertical series of samples were collected during the summer of 1951, one on July 20 and the other on August 16. These were approximately the same dates of collection as in the previous summer. The first of these series showed a yield of 20,213 and the second 30,936 units per liter. In both, Chrysophyceae were the most abundant constituting 56.1 and 82.6 percent respectively. In the first crop, diatoms contributed 36 percent and in the second only 8 percent. The remainder consisted of blue-greens and Dinophyceae.

Considering all the standing crops appearing during three summers, the Chrysophyceae were the most abundant, constituting an average of 53.5 percent of the total. Diatoms were second making up an average of 27.4 percent. Blue-greens and Dinophyceae were third and fourth contributing 30.5 and 28.6 percent respectively.

Fig. 13 demonstrates the vertical distribution of the phytoplankton in Lancaster Lake. Most of the phytoplankton occurred in the epilimnial layer during the period of thermal stratification. This illustrates the decided effect of thermal stratification on vertical distribution of phytoplankton.

MUNRO LAKE

Because this lake is shallow and susceptible to wind action, it would be expected that the phytoplankton would be distributed uniformly from top to bottom. Generally speaking, this was the case. Five vertical series of samples were collected at different times during the summer of 1948 and two during each of the summers of 1950 and 1951. At no time in 1948 and 1950, when samples were collected, was there a pulse. The smallest standing crop during these two summers amounted to 2,549 and the largest to 37,353 units per liter, the latter occurring in 1950. During the summer of 1951, the first vertical series of samples taken did not give evidence of a pulse but the second series, collected on August 15, represented a small pulse amounting to 82,867 units per liter.

From the standpoint of the various classes of algae comprising the total population of phytoplankton and considering the three summers as a whole, blue-greens were most abundant, making up an average of 58.5 percent. Diatoms were the next most abundant with 21.4 percent. Only in one series, collected on July 27, 1950, were the diatoms more abundant than the blue-greens; the diatoms constituting 58.5 percent and the blue-greens only 21.3 percent. The third largest contributors were the Chrysophyceae (consisting exclusively of *Dinobryon*) with 14.4 percent. The Dinophyceae amounted to 4.8 percent and the green algae only one percent.

Welch (1938a) enumerated phytoplankton samples taken from Munro Lake during the summers of 1932 and 1936. Interestingly enough, the standing crops occurring during each of those two summers were very similar quantitatively and qualitatively to those analyzed during the present study. Blue-greens were the most abundant and green algae the least abundant during those two summers also.

VINCENT LAKE

Vertical series of plankton samples were also collected from Vincent Lake during the summers of 1948, 1950 and 1951 and with the same frequency as from Munro Lake; i.e., five series were collected in 1948 and two during each of the summers of 1950 and 1951. Vincent Lake, like Munro Lake, is relatively shallow and thermal stratification, when it occurs, persists for only short periods of time. Thus, as would be expected, the phytoplankton were distributed fairly uniformly from surface to bottom. The standing crops during these three summers varied in amounts ranging between 22,613 and 48,875 units per liter, none of them being large enough to be called a pulse.

In Vincent, as in Munro Lake, the blue-green algae were the most abun-

dant, averaging 66.9 percent of the total. The Dinophyceae, composed only of *Peridinium*, contributed an average of 17.3 percent while the green algae made up 13.5 percent. The diatoms were very poorly represented in this lake making up only 1.7 percent and the Chrysophyceae occurred in negligible amounts composing less than one percent of the population.

Phytoplankton counts of samples collected from Vincent Lake during the summer of 1936 were reported by Welch (1938). During that summer, the largest group of phytoplankters was the green algae composed mainly of a certain species of *Staurastrum*. This single species appeared in amounts ranging between 250,000 and 460,000 organisms per liter. Blue-greens were the least abundant, occurring in very small numbers. It is apparent that there are considerable quantitative differences between these crops and those observed by the present writer fourteen years later. The green algae have certainly decreased in number while the blue-greens have increased to become the greatest contributors to the phytoplankton populations.

LAKE LANSING

Five vertical series of plankton samples were collected from this lake at different times during the fall season of 1950. The standing crops during this period of time occurred in amounts ranging between 15,831 and 39,819 units per liter, never reaching the status of a pulse.

The first series was taken on August 28 and it represented the smallest yield which was observed during this entire season. On that day, thermal stratification, although not very marked, was still present, and examination of the vertical distribution of the phytoplankton indicated that most of the population was in the epilimnial region (fig. 14). The second series was collected one week later on September 4. At that time the fall overturn was in progress and the phytoplankton as a whole had begun to increase, even though their population had been distributed almost uniformly from surface to bottom. The remaining series of samples indicated a general increase in the population of the phytoplankters as the season progressed in addition to their fairly uniform vertical distribution.

The phytoplankton of this lake, during the fall season, was composed mainly of diatoms, blue-green algae and Dinophyceae whose average contributions to the total were 51 percent, 34.4 percent and 13.7 percent respectively. The green algae and Chrysophyceae together constituted less than one percent. Those series which were collected during August and September showed that for those two months, each of the three classes contributed approximately equal
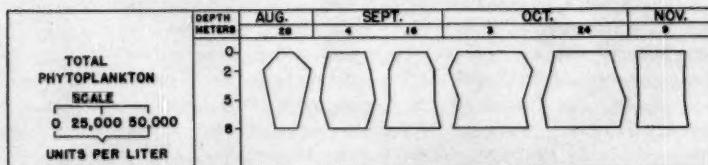
Fig. 14.—Vertical distribution and variation in standing crops of phytoplankton and their percentage composition in Lake Lansing during the fall of 1950.
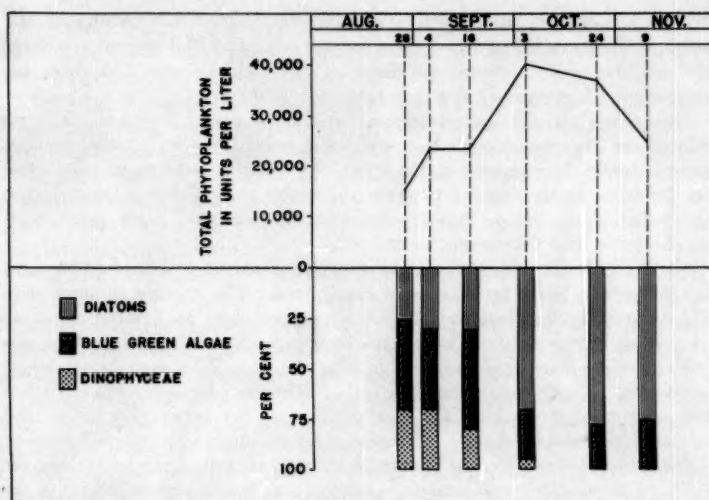
Fig. 15.—Variation in standing crops of phytoplankton and their percentage composition in Lake Lansing during the fall of 1950.

percentages to the population (fig. 15). Those series collected during October and November, however, included hardly any Dinophyceae. The crops during the latter two months contained between 70 and 75 percent diatoms and between 25 and 30 percent blue-green algae.

COMPARISON OF PHYTOPLANKTON POPULATIONS IN THE FIVE LAKES

Although plankton samples were taken from Douglas Lake through 16 consecutive months, nevertheless, the summer seasons of 1948, 1950 and 1951 were the only times during which samples were collected from all four of the northern lakes (Douglas, Lancaster, Munro and Vincent). It is for this reason that only the summer production of phytoplankton from these lakes will be compared. An average of the mean summer standing crops of phytoplankton for the three summers was calculated for each lake, these values being derived for the total phytoplankton and each of its major groups (table 15). It is these values for the different lakes which will be used in the comparison just mentioned.

Vincent Lake produced, on the average, the largest number of phytoplankters, having 36,010 units per liter. Douglas Lake ranked second with 32,742 units per liter while Munro and Lancaster came third and fourth with 23,166 and 14,310 units per liter respectively.

Douglas Lake yielded 20,726 units of diatoms per liter which was the largest diatom production amongst these lakes. In Douglas Lake it happened to be 63.3 percent of the entire crop. Lancaster and Munro each produced

about 6,000 units per liter, however in Lancaster Lake, this amount was 41.8 percent of the total, whereas in Munro Lake it was only 29.6 percent. Vincent Lake was the poorest diatom producer of all, yielding only 661 units per liter, a mere 1.8 percent of the crop.

The green algae did not seem to be abundant in any of the lakes. Vincent produced the largest number which was 5,158 units per liter, but this amount constituted only 14.3 percent of the total. In Douglas Lake there were 1,094 units per liter constituting 3.3 percent. Lancaster and Munro produced even fewer green algae, but in neither of the latter lakes did these green algae comprise more than 0.1 percent of the total.

Vincent Lake, in addition to producing the greatest number of green algae also ranked first in the production of blue-greens. The average summer yield of blue-greens in this lake was 23,200 units per liter, an amount equal to 64.4 percent of the total. The second largest production of blue-greens was 13,646 units per liter, which occurred in Munro Lake. This amount comprised 58.9 percent of all the phytoplankton in Munro. Douglas Lake yielded 2,808 units per liter which was 8.6 percent of the entire population and Lancaster Lake contained only 929 units per liter which was only 6.5 percent.

The Dinophyceae were not present abundantly in any of the lakes, however the lake that produced the greatest number was Vincent with 6,758 units per liter. This amount made up 18.8 percent of Vincent's total crop. Douglas Lake contained 1,390 units per liter which amounted to only 4.2 percent. Both Lancaster and Munro, each produced about 600 units per liter and in both cases, this number comprised between three and four percent of their totals.

With regard to the Chrysophyceae, Lancaster and Douglas lakes each yielded about 6,800 units per liter; however, in Lancaster this amount equalled 47.7 percent of the total whereas in Douglas it constituted only 20.6 percent. Another difference was that in Lancaster this group was composed almost entirely of *Synura* while in Douglas Lake it was made up exclusively of

TABLE 15.—Average of the three mean summer standing crops of phytoplankton and their percentage composition for 1948, 1950 and 1951 in Douglas, Lancaster, Munro, and Vincent lakes.

	Douglas Lake	Lancaster Lake	Munro Lake	Vincent Lake
Diatoms count	20,726	5,983	6,854	661
Percentage	63.3	41.8	29.6	1.8
Green algae count	1,094	18	175	5,158
Percentage	3.3	0.1	0.8	14.3
Blue-green algae count	2,808	929	13,646	23,200
Percentage	8.6	6.5	58.9	64.4
Dinophyceae count	1,390	556	675	6,758
Percentage	4.2	3.9	2.9	18.8
Chrysophyceae count	6,724	6,824	1,816	233
Percentage	20.6	47.7	7.8	0.6
Total count*	32,742	14,310	23,166	36,010

* Count in units per liter.

Dinobryon. Munro Lake contained 1,816 units per liter which was 7.8 percent of the total and Vincent Lake contained 233 units per liter which was only 0.6 percent.

By way of summary, then, Douglas Lake produced the largest diatom population while Vincent Lake was responsible for the largest number of green algae, blue-greens and Dinophyceae. Both Lancaster and Douglas lakes must share equally the honor of yielding the greatest number of Chrysophyceae although Lancaster produced about 100 more units per liter than did Douglas Lake. The poorest producer of both diatoms and Chrysophyceae was Vincent Lake.

Plankton samples were collected from Lake Lansing during the fall of 1950 and hence it is possible to compare the mean fall standing crop of Lake Lansing with that of Douglas Lake for the year 1950 (table 16). Douglas Lake was the greater phytoplankton producer, yielding 57,581 units per liter as compared to 27,775 units per liter from Lake Lansing.

Diatoms appeared as the largest group in both lakes amounting to 52,868 units per liter in Douglas and 15,821 units per liter in Lake Lansing. In the former lake, this amount constituted 91.8 percent and in the latter 57.0 percent of their respective totals. The green algae occurred in very small numbers in both lakes, 887 in Douglas and 106 units per liter in Lake Lansing, neither number comprising more than 1.5 percent in either lake. The blue-greens were more abundant in Lake Lansing with 8,864 units per liter, an amount which equalled 31.9 percent of the total crop of that body of water. Douglas Lake on the other hand, contained only 3,236 units of blue-greens per liter which made up 5.6 percent. Lake Lansing ranked first in the production of Dinophyceae, yielding 2,972 units per liter which amounted to 10.7 percent of the total. The population of Dinophyceae in Douglas Lake was so small that it might be considered negligible both in actual units of count per liter and from the standpoint of percentage of the total population. The production of Chrysophyceae was negligible in both lakes.

In general, then, Douglas Lake produced the greater number of diatoms

TABLE 16.—Comparison of the mean fall standing crops of phytoplankton and their percentage composition for 1950 in Douglas Lake and Lake Lansing.

	Douglas Lake	Lansing Lake
Diatoms count	52,868	15,821
Percentage	91.8	57.0
Green algae count	887	106
Percentage	1.5	0.4
Blue-green algae count	3,236	8,864
Percentage	5.6	31.9
Dinophyceae count	540	2,972
Percentage	0.9	10.7
Chrysophyceae count	50	12
Percentage	0.1	0.0
Total count*	57,581	27,775

* Count in units per liter.

although diatoms were the most abundant group in each of the lakes. Lake Lansing yielded more blue-greens and more Dinophyceae than did Douglas Lake. Both lakes were poor producers of green algae and Chrysophyceae.

DISCUSSION OF THE INDIVIDUAL GENERA OF PHYTOPLANKTON

The following is a detailed description of the population trends of each of the genera observed in the phytoplankton of the five lakes investigated. The results of the actual counts of these genera are not included in this paper. They have been tabulated and microfilmed and are available at University Microfilms, Ann Arbor, Michigan (Tucker, 1952).

Asterionella was found in all the lakes except Vincent. During the summer of 1948 this genus appeared in all the standing crops from Douglas Lake, ranging in amounts from 300 to 3,410 units per liter. During the summer of 1950 in the same lake the number of *Asterionella* in the standing crops varied between 940 and 5,565 units per liter. Shortly after the beginning of the fall overturn, which occurred sometime between September 16 and October 2, they started to increase and reached their maximum peak on November 14 at which time they were present in the amount of 85,920 units per liter. This *Asterionella*-peak constituted the largest part of the phytoplankton pulse at that time. By February 26, 1951, their number had decreased to 290 units per liter. From that date to June 21, their population did not exceed 4,010 units per liter. On July 9 a more abundant yield of *Asterionella* was noted amounting to 16,570 units per liter, but this abundance did not persist and on July 23 it had decreased to 1,260 units per liter. The remainder of the summer saw variations between 30 and 1,140 units per liter, but on October 6, shortly after the beginning of the fall overturn of 1951, their number had increased to 46,380 units per liter. Field work was terminated on that day, so it is not known whether their numbers continued to increase or whether this amount was the maximum in that particular peak. In Douglas Lake, then, *Asterionella* had one main bloom in each of the years 1950 and 1951, occurring shortly after the fall overturn (fig. 10).

Lancaster produced practically no *Asterionella* during the summer of 1948, but in the summers of 1950 and 1951 the standing crops contained this genus in amounts ranging between 375 and 6,525 units per liter, approximately the same range as in Douglas Lake for the same periods. In Munro Lake, *Asterionella* appeared only twice during three summers and its number in each of the crops in which it appeared did not exceed 225 units per liter. During the fall of 1950, the Lake Lansing phytoplankton contained this genus in amounts ranging from 450 to 9,163 units per liter while Douglas Lake, for the same period, produced *Asterionella* in amounts ranging from 735 to 85,920 units per liter.

Fragilaria occurred in all of the lakes except Vincent. In Douglas Lake during the summer of 1948, the population of this genus varied from 229 to 775 units per liter. Except for two dates in the 16 month period of investigation carried on in Douglas Lake between July 3, 1950, and October 6, 1951, all of the yields of *Fragilaria* contained amounts varying between 35 and 8,960 units per liter. The two dates referred to were July 3, 1950, at which

time this genus occurred in the amount of 52,520 units per liter and October 6, 1951, the crop that day being 14,050 units per liter. The former of the two crops probably represented the ending of a peak whereas the latter was part of a general pulse beginning at about that time. Although the yields of the majority of the crop of *Fragilaria* from Douglas Lake during the 16 month period of investigation are included in the range previously mentioned, it should be added that the yields, which occurred shortly after each of the overturns, tended to equal amounts near the upper part of the range (fig. 10).

During the three summers of 1948, 1950 and 1951, *Fragilaria* occurred in all of the standing crops observed in Lancaster Lake in amounts varying between 125 and 1,913 units per liter except on one occasion in 1950 at which time *Fragilaria* consisted of 31,288 units per liter. In Munro Lake, this genus appeared only twice during the entire three summers and at neither of these times did it exceed 18 units per liter. During the fall of 1950 the number of *Fragilaria* appearing in the crops of Lake Lansing, varied between 1,038 and 3,394 units per liter. In Douglas Lake during the same period this genus occurred in amounts ranging between 1,800 and 8,340 units per liter, the majority of the crops containing amounts near the higher end of the range.

Melosira was present in all of the lakes. In Douglas Lake, during the summer of 1948, it occurred in amounts ranging from 266 to 1,237 units per liter. During the 16 month period of investigation in Douglas Lake, including the summers of 1950 and 1951, the population of this genus varied quantitatively from 39 to 24,880 units per liter. The general trend of these population changes followed that of the quantitative changes in the total diatoms (fig. 10). The greatest numbers of *Melosira* occurred shortly after the inception of the spring and fall overturns whereas the smallest amounts occurred during the midsummer periods and during midwinter under the ice cover.

In Lancaster Lake, *Melosira* appeared in only one series of samples during the three summers. That was on July 20, 1950, and the amount was 38 units per liter. Munro Lake contained this genus in most of the series taken during the summers of 1948, 1950 and 1951, however, there were three series in which it did not appear. Even when it occurred, it did so in small amounts varying between 50 and 250 units per liter. *Melosira* appeared only three times in Vincent Lake during the three summers and in quantities between 50 and 100 units per liter. In Lake Lansing during the fall of 1950, its population varied between 875 and 3,850 units per liter, whereas in Douglas Lake for the same period, this genus occurred in amounts ranging between 2,490 and 22,890 units per liter. *Melosira* occurring in Douglas Lake during the fall of 1950, however, were present in amounts more closely resembling those in the upper end of the range.

Navicula appeared in the phytoplankton yields from each of the lakes, however never abundantly. It occurred consistently in Douglas, Munro, and Lake Lansing, but only rarely in Lancaster and Vincent lakes. In Munro Lake it appeared in amounts between 100 and 2,300 units per liter. Considering all of the crops from each of the other four lakes, only once did *Navicula* occur in an amount exceeding 460 units per liter; that being in Douglas Lake on May 10, 1951, at which time its population consisted of 2,634 units per liter.

Stephanodiscus occurred in most of the crops from each of the lakes. Although the yields in Douglas Lake were highest after the spring and fall overturns, they never exceeded 3,354 units per liter at any time. None of the crops from any of the other four lakes contained this genus in amounts greater than 775 units per liter.

Synedra was found in plankton samples from all of the lakes. In Douglas Lake during the summer of 1948, its numbers never exceeded 800 units per liter. During the 16 month period of investigation, the population changes of *Synedra* simulated the population changes of the total diatoms and contributed noticeably to the diatom pulses (fig. 10). On July 3, 1950, this genus was present in the amount of 5,860 units per liter. This number gradually decreased and on September 16 the phytoplankton contained only 990 units of this phytoplankton per liter. The fall overturn of 1950 started a few days later and at the same time the population of *Synedra* began to increase. On November 14, its maximum peak consisting of 14,010 units per liter was observed. Following this a gradual decrease occurred and the population remained small under the ice, reaching a low of 2,120 units per liter. After the break up of the ice and during the spring overturn, the population began to increase in size. Two peaks then occurred, one on May 10, 1951, with 23,300 units per liter and the other on July 9 with 12,995 units per liter. These two peaks were separated by small crops occurring in June whose amounts varied between 2,760 and 3,020 units per liter. After the second peak the number of *Synedra* began to decrease and continued to do so until on September 15 it was only 4,360 units per liter. On October 6, shortly after the beginning of the fall overturn of 1951, there were sufficient numbers of *Synedra* in the standing crop to indicate the beginning of another peak. On that day Douglas Lake contained 14,010 units of this genus per liter.

Lancaster and Vincent lakes appeared to be poor producers of *Synedra*. None of the crops observed in either of these lakes during the three summers contained more than 1,500 units per liter. Very few *Synedra* were observed in Munro Lake during the summer of 1948; only between 50 and 300 units per liter. In the summers of 1950 and 1951, however, several of the crops from that lake were quite large ranging from 675 to 32,775 units per liter. Lake Lansing during the fall of 1950 produced *Synedra* in amounts varying between 713 and 23,725 units per liter. Douglas Lake during the same period of time produced this genus in amounts ranging from 750 to 14,010 units per liter.

Tabellaria occurred in all of the lakes with the exception of Lake Lansing. In Douglas Lake during the summer of 1948 it appeared in amounts ranging between 330 and 1,280 units per liter. During the first two weeks of July, 1950, the standing crop of *Tabellaria* in Douglas Lake decreased from 55,470 to 8,488 units per liter. From that time until October 6, 1951, the crops contained quantities of this genus ranging from 660 to 8,950 units per liter. Those yields of phytoplankton appearing after the fall and spring overturns contained the largest number of *Tabellaria*, whereas those occurring during midsummer and midwinter contained the least number. Lancaster, Munro and Vincent lakes often did not contain this genus. However, there were at

least two crops from each lake that did contain it, but never in amounts exceeding 250 units per liter.

Anabaena was found in all of the lakes except Vincent but never in great abundance. In Douglas and Lancaster lakes it occurred on occasion but in neither lake did it exceed 231 units per liter. The yields from Munro Lake contained between 24 and 1,275 units of *Anabaena* per liter, whereas Lake Lansing contained slightly larger populations ranging from 738 to 3,375 units per liter.

Aphanizomenon was observed only in Munro Lake. It appeared once during the summer of 1948 and once during the summer of 1950; neither time did it exceed 10 units per liter.

Chroococcus appeared only in Lancaster, Munro and Vincent lakes, and not regularly. None of the crops from either Lancaster or Vincent Lake contained more than 663 units per liter. Munro Lake, on the other hand, contained this genus in amounts ranging from 250 to 19,800 units per liter.

Coelosphaerium occurred in all of the lakes except Munro. In Lancaster and Vincent lakes it appeared in only a few instances, never exceeding 100 units per liter. In Douglas Lake, it occurred in all the series of samples except in those taken in the winter under the ice cover. The summer and fall crops from Douglas Lake contained *Coelosphaerium* in amounts varying between 360 and 1,680 units per liter. Lake Lansing contained it in quantities varying between 206 and 2,250 units per liter.

Merismopedia occurred in all of the lakes except Lancaster. Douglas Lake contained it only in the summer when it occurred in amounts ranging from 1 to 240 units per liter. Only a few of the crops from each of the other three lakes contained *Merismopedia* and in amounts never exceeding 89 units per liter.

Microcystis appeared in all of the five lakes. Douglas Lake contained quantities varying between 117 and 8,280 units per liter; the larger crops occurring shortly after the fall and spring overturns and the smaller ones during midsummer and midwinter. In Lancaster Lake, the phytoplankton contained this genus in amounts ranging from 181 to 1,319 units per liter. Munro and Vincent lakes produced *Microcystis* more abundantly than did the other lakes with amounts ranging from 1,200 to 41,600 units per liter in Munro and 14,250 to 33,475 units per liter in Vincent. Lake Lansing contained quantities varying between 4,888 and 7,200 units per liter.

Oscillatoria was observed only in Douglas Lake and Lake Lansing. In the former it occurred infrequently, never exceeding 120 units per liter. In Lake Lansing, only a few of the crops contained *Oscillatoria* and in amounts never larger than 150 units per liter.

Arthrodesmus was observed in Douglas, Lancaster and Vincent lakes. In the first two, it appeared only two or three times during each summer and in amounts not greater than 150 units per liter. In Vincent Lake, however, it appeared consistently in amounts ranging from 150 to 3,675 units per liter.

Cosmarium occurred in several of the crops from Douglas Lake in quantities between 20 and 520 units per liter. It appeared once in Lancaster Lake during the three summers in the amount of 38 units per liter and once in Lake Lansing during the fall of 1950 in the amount of 75 units per liter.

Dictyosphaerium was found only in the Lake Lansing samples. It occurred twice during the fall of 1950, each time in the amount of 19 units per liter.

Eudorina was present in Lancaster, Munro and Lake Lansing. It appeared in only one or two crops from each of these lakes and never exceeded 158 units per liter.

Pediastrum was present in each of the five lakes. Douglas Lake contained it in nearly every crop in numbers varying between 20 and 600 units per liter. It occurred only once or twice in each of the other lakes, never exceeding 200 units per liter.

Scenedesmus was found in Douglas, Munro and Vincent lakes but it appeared seldom in any of them and in amounts not greater than 150 units per liter.

Staurastrum appeared in all of the lakes except Lancaster. In Douglas Lake it occurred in most of the crops but only exceeded 2,660 units per liter once. That was on July 3, 1950, at which time the yield was 8,020 units per liter. In Munro and Lansing lakes it occurred rarely, and never in amounts larger than 100 units per liter. Vincent Lake seemed to be the greatest producer of this genus. It was present consistently in amounts ranging from 150 to 9,150 units per liter. During the summer of 1936, according to Welch (1938), this genus occurred in Vincent Lake in amounts ranging from 200,000 to 460,000 phytoplankters, and was the most abundant of all the genera in the lake.

Tetraedron was found only in Lake Lansing. It appeared in just two crops and in neither of these did it exceed 56 units per liter.

Xanthidium occurred only in Vincent Lake. It was observed in just three instances and in none of them did it exceed 300 units per liter.

Dinobryon was found in all of the lakes. In Douglas Lake it was the only representative of the class Chrysophyceae and appeared in amounts varying between 20 and 89,650 units per liter. The large crops of this genus occurred shortly after the spring overturns and persisted for two or three weeks into the periods of thermal stratification, thus contributing to the major phytoplankton pulses which occurred during those times. There was not any appreciable increase in production of *Dinobryon* after the fall overturns. In between the times of maximum abundance this genus appeared in very small numbers; sometimes it was absent.

In Lancaster Lake, during the summers of 1948 and 1950, this genus appeared in amounts varying between 100 and 2,323 units per liter. In the summer of 1950, however, it occurred in much larger numbers ranging from 11,225 to 14,050 units per liter. Although *Dinobryon* appeared in nearly all of the crops from Munro Lake, still it never appeared abundantly but in amounts between 100 and 4,500 units per liter. The largest yield observed in Vincent Lake was 1,050 units per liter. In Lake Lansing it appeared only once and in the amount of 75 units per liter.

Synura was found only in Lancaster Lake but here it occurred more abundantly than any of the other genera; at least in the summer months during which these observations were made. It appeared in amounts ranging between 113 and 11,488 units per liter.

Ceratium appeared in all the lakes except Vincent. In Douglas Lake, its

number varied between 30 and 3,360 units per liter. The larger amounts occurred shortly after the overturns and persisted for several months while the smaller yields were produced during the winter months. Lancaster Lake produced this genus quite consistently during the summer months in small amounts ranging from 50 to 925 units per liter. *Ceratium* was also found in Munro Lake in most of the series of samples, but here, too, in small numbers from 50 to 700 units per liter except in one instance in 1950 when it was present in the amount of 2,850 units per liter. In Lake Lansing during the fall of 1950, this phytoplankter appeared in quantities between 50 and 7,388 units per liter. The larger populations occurred in August and September whereas the smaller ones were produced in October and November.

Peridinium was found in all of the lakes except Lake Lansing. In Douglas and Munro lakes it appeared in most of the series of samples but in neither lake did it exceed 220 units per liter. Lancaster also produced it in small quantities, never more than 775 units per liter. Vincent Lake, on the other hand, contained large numbers of *Peridinium* ranging between 50 and 16,950 units per liter.

DISCUSSION

The question of relationship between the numerical abundance of phytoplankton and the nature of their chemical environment has been the object of many investigations both in this country and abroad. Such studies have produced some tangible results and considerable basis for speculation and hypotheses pointing to the need for further investigation.

Atkins (1923) concluded that phosphorus might be a limiting factor in the production of phytoplankton in the sea. Prescott (1931) states that he has "found positive correlations between phosphorus content and productivity of plankton in Iowa lakes." He further states that "there is some evidence that the difference between one eutrophic lake and another in respect to its flora might be due to the difference in phosphate content." In some of the Wisconsin lakes, however, there was no evidence that phosphorus was a limiting factor to growth of phytoplankton populations (Juday, Birge, Kemmerer and Robinson, 1927; Juday and Birge, 1931; and Tressler and Domogalla, 1931). In Douglas Lake, which was studied quite intensively by the present author, the soluble inorganic phosphate fluctuated irregularly in the epilimnial waters during the 16-month period of investigation (fig. 3, part I) but these fluctuations seemed to have no relationship with the occurrence of spring and fall phytoplankton pulses.

There are some who believe that nitrates have a controlling influence on phytoplankton productivity, among them Prescott (1939) who found direct correlations between nitrogen and quantity of plankton in the various lakes which he studied. Riley (1940), on the other hand, concluded that in Linsley Pond nitrates and phosphates appeared to have no effect on productivity although they are closely related to variations in the standing crop. Still others suggest that changes in the ratio of nitrates to phosphates may be responsible for differences in the magnitudes of the phytoplankton populations (Pearsall, 1932; Cooper, 1937; and Hutchinson, 1941). Nitrates were not determined in the present investigation and hence it is not known whether nitrogen is related to changes in numbers of phytoplankters in Douglas Lake.

Both Pearsall (1932) and Hutchinson (1944) have suggested certain relationships between chemical changes in the water and the periodicity of certain phytoplankters. Pearsall maintained that in the English lakes, diatoms occur when the waters are richest in nitrate, phosphate and silica. He also postulated that diatoms cannot reproduce appreciably when the concentration of silica is less than 0.5 mg per liter. Lund (1950) found a positive correlation between available silica and size of populations of *Asterionella*. He also confirmed the view of Einsele and Grim (1938) that the amount of silica per unit area of cell is constant under all conditions. In the light of these facts, he agreed with Pearsall's hypothesis pertaining to silica and concluded that this element could very well be a limiting factor to the production of diatoms. He did not, however, make the same committment regarding phosphorus because he found that cells of *Asterionella* can store phosphorus in excess of immediate requirements even when the concentration in the water is one microgram per liter or less. If such is the case with other phytoplankters, then a measurement of the available soluble inorganic phosphorus in a lake would give no indication as to whether or not the plankton are starved for phosphorus. Hutchinson (1944) found the water of Linsley Pond adequately supplied with phosphorus, nitrogen and silica but poor in diatoms and hence feels rather doubtful of Pearsall's hypothesis.

The populations of *Dinobryon* in certain English lakes (Pearsall, 1932) begin to grow with a rise in the ratio of nitrate to phosphate and with a decrease in the amount of silica in the water. In Linsley Pond, Hutchinson (1944) found that an increase in the number of *Dinobryon* was associated with a rise in the ratio of nitrate to phosphate, as pointed out by Pearsall, but not with a decrease in silica. The data of Tressler and Domogalla (1931) gave no evidence that a change in the nitrogen-phosphorus ratio had any effect on the variations of *Dinobryon* populations in Lake Wingra, however, a decrease of the silica content of the water was observed to occur simultaneously with an increase in the quantities of this genus.

Pearsall (1932) also noticed that a fall in calcium seemed to favor an increase in the numbers of *Dinobryon*. In the present study, the data from Douglas Lake showed that a decrease in bicarbonates accompanied the reduction in the quantities of *Dinobryon* during the first few weeks of July, 1950, and an increase of bicarbonates occurred when populations of this genus were growing during the first two weeks of May, 1951. If it can be implied that variations in bicarbonates indicate similar variations in calcium, then the relationship between calcium and *Dinobryon* populations in Douglas Lake is the reverse of that in the English lakes and it might be inferred that in Douglas Lake it is an increase rather than a decrease of calcium that is favorable for a greater rate of reproduction among the members of this genus. Pearsall (1932) and Hutchinson (1944) found that *Dinobryon* did not appear until after the decline of the diatom maximum. In Douglas Lake, the diatom and *Dinobryon* maxima occurred simultaneously in the same spring pulse, indicating therefore, the presence of sufficient nutrients in the water at that particular time to support both populations.

The abundance of blue-green algae has been correlated with high concentration of organic matter (Pearsall, 1932). In the present investigation, blue-

greens were found to be most numerous in Vincent Lake, a body of water rich in organic matter. Pearsall also found that large populations of blue-greens were maintained in the English lakes despite minimal quantities of nitrate and phosphate. Vincent Lake, although containing more total phosphorus per liter than any of the other lakes here studied, nevertheless contained the least amount of available inorganic phosphorus, usually less than one microgram per liter.

Very little is known of the chemical factors controlling the population growth of green algae in natural waters. Pearsall (1932) concluded that more green algae occur during periods when concentrations of nitrates and phosphates in the waters are low. He further states that in the English lakes there seems to be no general correlation between abundance of green algae and the amount of organic matter. Certain individual species from this group (for example, *Eudorina elegans*) however, appear to thrive in this type of environment. In the present study, although green algae were not found to be abundant in any of the lakes, their largest population appeared in Vincent Lake which, incidentally, was the same lake containing the largest number of blue-greens.

Vincent Lake is an interesting body of water for several reasons. Part I, the section dealing with the chemical conditions of this lake, mentions the fact that the hydrogen ion concentration of the water had been changing during the past 30 years. Whereas the water used to be on the acid side of the pH scale, it is now neutral and often a little on the alkaline side. This change in pH, of course, is merely an index of the occurrence of other changes in the chemical nature of the lake. During the summer of 1936, a certain species of *Staurastrum* predominated the plankton populations with its large numbers. During that same summer, blue-greens were in the minority. During the summer of 1951, some 15 years later, this *Staurastrum* appeared in very small numbers, whereas, the quantities of blue-greens had increased tremendously to become the largest group in the total population. A possible explanation for this change in the algal flora is the change in the chemical environment.

Another species found in Vincent Lake worthy of comment was *Peridinium wisconsinensis*. This phytoplankter comprised approximately 17 percent of the mean summer standing crop of the lake. It did not appear in any of the other lakes in this investigation, but it was observed by the writer in Weber Lake, a small body of water in northern Michigan. The chemical characteristics of Weber Lake were similar to those of Vincent Lake with respect to the pH, which was slightly on the acid side, and the bicarbonate content, which was extremely low. If this species of *Peridinium* is found in other bodies of water having the same chemical characteristics, it might prove to be a useful biological index.

It is evident from the discussion thus far, that many inconsistencies exist between the behavior of similar phytoplankters in different lakes, and hence clear cut correlations between phytoplankton abundance and chemical factors can not be indicated. The reasons for many of these inconsistencies are still in the realm of speculation, although several of them are known. It is known, for instance, that the physiological state of the cell at the time of analysis

could have a profound influence on the results obtained. It is also realized that where a single factor in itself may not exert an influence on the reproductive rate of a cell, two or more factors might act synergistically. Another possible reason for these inconsistencies could be the degree of competition between species for the available nutrients. Still another aspect which should be considered is the effect of predators on the phytoplankton populations. All of these factors plus many more could contribute to the dynamics of a single ecological situation. The relationships and interrelationships are very complex. The ecologist is becoming increasingly aware of the fact that observations in the field can produce only limited information and that biological situations must be carried from the field to the laboratory where variables can be isolated and observations made with greater precision, through the medium of controlled experiments.

Although no clear cut correlations could be established between variations of phytoplankton numbers and changes in chemical factors of the environment, the writer feels that a discussion of the sequence of events preceding each plankton pulse might express some cause-effect relationships. In Douglas Lake, each pulse occurred almost immediately after the beginning of the overturns. It is certainly not a new concept that during circulation of the water, nutrients which have been accumulating at the bottom are brought to the surface and made available to the existing plankton, and that these nutrients stimulate the phytoplankters to reproduce at a greater rate. What are the conditions in the hypolimnion of Douglas or any other temperate lake of the second order? First of all, the bottom is covered with dead plankton organisms which have descended from the upper waters (Welch, 1935). These organisms are being decomposed by bacteria, and various elements such as phosphorus and nitrogen are being released (Waksman, 1941). As a result of the activity of these bacteria, the bottom of the lake eventually becomes depleted of oxygen. In Douglas Lake, toward the end of the summer, oxygen was absent in the bottom of the hypolimnion, however the phosphorus which was supposedly being released from the decomposing plankton could not be detected even at the bottom of the lake until approximately eight weeks after the oxygen had disappeared.

The logical question to ask at this time is: "What happened to the phosphorus that was being released as a result of the decomposition of the dead plankton organisms at the bottom of the lake?" In order to answer this question, it is necessary to have an appreciation of some of the many chemical reactions which are involved in the pelometabolism of the lake. Einsele (1938) was one of the first workers to investigate the chemical relationships which exist between the bottom mud, mud-water interphase and the free water. He found that divalent iron and phosphate can exist side by side in solution in the hypolimnetic waters only when oxygen is absent, but if oxygen is introduced, for instance at the fall overturn, the iron and phosphorus will combine to form an insoluble ferric phosphate precipitate which will sink to the bottom mud and become part of it. Conversely, when oxygen is removed from the water, the iron will be reduced to form ferrous phosphate which is soluble. The rates of these reactions are of course subject to the relative concentrations of the elements involved, plus various chemical factors in the environment

such as hydrogen ion concentration, the presence of hydrogen sulfide and perhaps others which as yet have not been discovered. Mortimer (1941) has produced evidence that phosphorus is strongly adsorbed on ferric hydroxide or ferric hydroxide organic complexes in the oxidized surface mud layers of lake bottoms as long as oxygen is present in the overlying water. When the oxygen becomes depleted, however, these ferric complexes are reduced and phosphorus is liberated into the water. Mortimer also conducted experiments in the laboratory to see if this phenomenon would occur in artificial mud-water systems. He took samples of typical lake-bottom mud and placed portions in each of three rectangular glass tanks, to which he later added lake water. The first tank was aerated regularly, the second left undisturbed but with the water surface exposed to air, and the third sealed from air with paraffin. When the dissolved oxygen had disappeared from the water in the sealed tank, Mortimer observed considerable increases in alkilinity, conductivity, ferrous iron, manganese, turbidity, silica and phosphorus. He also studied changes in the muds at the bottom of these tanks. In the first two tanks there were no increases in any of the elements and very little change in the composition of the muds. In the third, he found the behavior of the mud-water system very similar to those of the hypolimnial muds of certain lakes which he had studied.

Although Einsele and Mortimer describe different sets of reactions occurring in the hypolimnion at the time of oxygen depletion, it is probable that both sets of reactions are occurring simultaneously. In either case, however, none of the elements is released from the mud until the oxygen in the overlying water disappears.

In Douglas Lake, then, the dead plankton organisms decompose as a result of bacterial action, releasing phosphorus, nitrogen and other elements, but these either go into combination with iron to form insoluble precipitates or become adsorbed on ferric complexes. It is interesting to note that the bacteria are not only decomposing the dead organisms at the bottom of the lake but they are using up the oxygen, the presence of which inhibits the liberation of the elements which they are freeing.

During the summer of 1950, eight weeks elapsed from the time that oxygen disappeared from the bottom of the hypolimnion and phosphorus was released. This seemed to be rather a long delay but it is really not out of proportion when compared to similar time intervals in other lakes. Mortimer (1941) observed large-scale liberation of phosphate two or three weeks after the oxygen had fallen below one part per million. In his laboratory experiments, phosphate did not appear in large quantities until 40 to 50 days after the oxygen had fallen nearly to zero. Einsele and Vetter (1938) found that the steep rise in phosphate occurred normally one month after the oxygen had fallen to below one part per million. The time interval between oxygen depletion evidently varies considerably from lake to lake and probably depends upon the amount of ferric complex which has to be reduced, on the reducing capacity of the mud and on the conditions of microstratification near the mud surface which again depends on water movement. All this points to the conclusion that ferric complexes are only destroyed slowly by reduction, after which they liberate the adsorbed load of phosphorus.

It seems reasonable to assume that once the mud begins to liberate soluble inorganic phosphate into the water above, it would continue to do so, and that the supply of phosphate would keep building up in the bottom waters until oxygen is introduced at the overturn. In two instances such was not the case. In Douglas Lake, after the ice cover appeared in November, 1950, the phosphorus kept on increasing at the bottom and should have continued to increase until the spring overturn which occurred after the ice had broken up in April, 1951. However, between February 26 and March 28, although the ice cover was still present, there was a decrease of phosphorus from 33 to 15 micrograms per liter. In Lancaster Lake during the summer of 1951, after the oxygen had disappeared from the bottom, there was a continual increase of phosphorus. However, between August 16 and August 25, while the lake was still thermally stratified, there was a decrease from 175 to 130 micrograms per liter. This is a perplexing problem and at the present time there seems to be no plausible explanation. One possible answer might be that the sampling station was not located at exactly the same place each time. Mortimer (1941) and Hutchinson (1941) have evidence that turbulence occurs in the hypolimnion. If such is the case, then a very important factor to consider would be the position of the sampling stations relative to the deep holes. It is conceivable that variations in results may occur if samples taken on successive dates are not collected at exactly the same location in the lake.

Although cyclic fluctuations of phosphorus concentrations in the bottom waters of a lake can be expected throughout successive years, the heights of the peaks may not be identical. In Douglas Lake, peaks of phosphorus appeared in September of 1950 and 1951, however the former far exceeded the latter in size. The same factors are probably involved in the production of both of these peaks but a slight difference in their relationship to each other could very well alter the magnitude of the results. In this particular instance, however, the concentration of phosphorus occurring at the bottom on September 16, 1951, might not represent the maximum concentration during the time of phosphorus release. The periods of maximum liberation during the fall are evidently short, lasting from two to three weeks. If samples had been collected sometime between September 16 and Octobr 6, perhaps a higher peak might have been observed.

At the times of the overturns, the lake undergoes complete circulation from surface to bottom. It would be expected that elements which have been liberated at the botom up to this time will be distributed throughout the whole lake and become available to the phytoplankters in the upper waters, thus making it possible for them to reproduce more rapidly and form pulses. Determinations of phosphorus in the surface waters, therefore, should show a significant increase, if not in soluble inorganic phosphorus, at least in total phosphorus. The data in Douglas Lake indicate no such increase following the overturns.

A possible hypothesis which might explain these data is that although the water was being circulated vertically throughout the lake, the bottom phosphorus did not reach the upper waters. It is of interest to follow this argument through to its logical conclusion. As has already been mentioned, oxygen is absent in the hypolimnion just before the overturn. At the time

of the overturn, oxygen is reintroduced into the system and ferric hydroxide again formed. Some of the phosphorus is readsorbed on these ferric complexes and some recombines chemically with iron to form insoluble ferric phosphate. These combinations occur near the bottom of the lake where the elements other than oxygen have been accumulating. If these insoluble compounds are sufficiently heavy to sink to the bottom as soon as they are formed, without first being carried to the surface, they would not become available as nutrients to the plankton in the upper waters. This being true, it is necessary, then, to seek other sources of nutrients for these organisms. One possible source involves those plankters which die in the upper waters and undergo decomposition while descending, thus releasing certain elements directly into the upper waters. A difficulty inherent in this possibility at the present time, is the lack of information as to the rate of fall of the dead phytoplankters, and the rate of decomposition under aerobic conditions, both of which have to do with the rate of phosphorus release from the organisms. It is also possible, that as a result of wave action of the water against the shore, certain elements are leeched out of the soil of the slopes and are mixed into the upper waters. The supply of nutrients provided by these two sources to the epilimnial region would at least be continuous throughout the year, and if it is assumed that they provide sufficient food to maintain a phytoplankton population, then, factors other than amounts of nutrients must control the periodicity of phytoplankton in a lake such as Douglas. Furthermore, it must be admitted that it is merely coincidental that a phytoplankton pulse immediately follows an overturn, because the stirring action during an overturn is no different from that occurring almost constantly in the epilimnion, where the reproduction of phytoplankton takes place.

It seems unreasonable to assume that bottom phosphorus was not brought to the surface during the overturn. Water samples collected from the upper region of the lake while it was turning over, contained particles of bottom mud. Eggleton (private communication) has also observed particles of bottom mud in the surface water of a lake while it was in the process of an overturn. If the vertical stirring action of the water is capable of bringing these mud particles to the surface, surely it must be capable of carrying up molecules of ferric complexes which are much lighter. If it is postulated that bottom phosphorus was brought to the surface, then a different line of reasoning must be followed to account for the fact that data from Douglas Lake did not show an increase of this element following the overturn.

When oxygen is reintroduced into the system, it is true that the phosphorus becomes part of the newly formed ferric complexes and quite possibly some of these complexes do go back into the mud. The remainder is probably stirred vertically throughout the lake. As has been noted in figure 5 of Part I the phosphorus released from the bottom mud of Douglas Lake does not diffuse very far upward into the hypolimnion. The data collected just a short time before the overturn indicated that the high concentration of phosphorus had not risen beyond one meter above the bottom of the lake.

Considering the total phosphorus in Douglas Lake, and assuming that on September 16, 1950, its enormous concentration of 641 micrograms per liter was contained in a layer of water one meter thick at the bottom of the

hypolimnion (table 4, Part I), certain rough calculations can be made to determine how much should have reached the upper waters during the overturn. The depth of the lake at the collecting station is 20 meters. If calculations are made for a hypothetical vertical column of water 1 meter square by 20 meters high, with a concentration of 641 micrograms per liter of total phosphorus in the water between 19 and 20 meters, then, a uniform distribution of the contents of the bottom layer of water throughout the column should increase the concentration of total phosphorus at all depths by 32 micrograms per liter. This value would be high if applied to Douglas Lake for several reasons. First, the surface area of the lake is greater than the area of that part of the bottom covered by deoxygenated water, thus resulting in greater dilution, and second, the bottom layer of water at lesser depths would contain less phosphorus than was found in the bottom layer of water at this station, because according to Mortimer (private communication) horizontal turbulence causes the denser bottom waters to accumulate in the deeper holes.

For the sake of argument, suppose that the amount of total phosphorus in the upper waters of Douglas Lake was increased by 32 micrograms per liter during the overturn. This together with the amount already there would make a total of approximately 42 micrograms per liter. The fact remains, however, that on October 2, 1950, when the lake was in the process of complete circulation, the concentration of total phosphorus in the upper waters was not significantly different from the concentration prior to the overturn. When the station was visited about two weeks earlier (September 16) thermal stratification was still in existence and the phosphorus which had been accumulating at the bottom of the lake was still undisturbed. In other words, sometime during this 16-day period during which no observations were made the overturn began, and the phosphorus, which was supposedly brought to the surface as a result of the vertical stirring action in the water, must have disappeared.

The problem as to where and how phosphorus disappears from lake water is one that is puzzling many workers. Barret (1952) observed that the surface waters of certain northern Michigan lakes lost as much as 70 percent of the total phosphorus in only three days. This figure coincides with the theoretical loss of total phosphorus in the surface water of Douglas Lake if it is assumed that phosphorus reached the surface waters in the first place.

Of the 641 micrograms per liter of total phosphorus present in the lower waters of the hypolimnion on September 16, the fraction represented by soluble inorganic phosphorus was 460 micrograms per liter. At the overturn, it would be expected that this soluble inorganic phosphorus, coming into contact with oxygen during the circulation might be stirred into the upper waters as part of the ferric complexes. Hutchinson (1941) also suggests that during an overturn, part of the phosphate, normally determined as soluble, might really be in a suspended but acid soluble form. He found this to be true during the autumnal overturn in Linsley Pond.

A logical question at the present time would be: "Can the algae utilize the phosphorus in this insoluble form?" Harvey (1937) has evidence that marine diatoms can make use of suspended ferric compounds. There is a strong possibility, therefore, that other phytoplankters might also utilize it.

The introduction of phosphorus from the hypolimnion into the upper waters at the time of the overturn, may be compared to the artificial addition of phosphorus fertilizer to the lake. Many investigators who have experimented with artificial fertilization of lakes have noticed extreme losses of the added phosphorus but have been unable to trace its disappearance. Einsele (1941) describes how large quantities of superphosphate added to a certain lake disappeared within a few weeks after which time the phosphate content of the lake water was the same as before the addition of the fertilizer. He claimed that the phosphorus was stored by the phytoplankton but, despite this, no increase in phytoplankton occurred. Hayes *et al* (1950) introduced radioactive phosphorus into the lake in an attempt to trace its disappearance. On the basis of this work Hayes (1951) suggests: ". . . that what seems to be a great deal of nutrient material (in terms of water) is really only a small fraction of an equilibrated system of water and solids." When nutrient material is added to the lake it does not disappear but rather it will partition itself between water and solids so that neither phase will be much richer than before. He claims that there is ". . . a continuous exchange of phosphorus going on between the water and solids in the lake, solids referring to plants and animals as well as a thin layer of participating mud, perhaps one mm. thick." He further concludes that if nutrient salts are added to a lake as fertilizer, within a few weeks 90 percent of them would be expected to enter the water-and-solid-phase and hence would not be detected by ordinary analyses. The remaining 10 percent is likely to remain in the water and contribute to the initiation of the algal growth.

The discussion thus far appears to strengthen the inference that phosphorus might have been brought to the upper waters of Douglas Lake during the fall overturn and had disappeared by October 2. It is unfortunate that, due to practical difficulties, daily analyses could not be carried out during the critical period between September 16 and October 2, 1950. Had this been possible, the question as to whether phosphorus was brought to the upper waters could be answered by fact rather than speculation.

One fraction of the total phosphorus which has not yet been mentioned is the organic sestonic phosphorus which is part of the protoplasm of plankton cells. In Douglas Lake during the fall overturn, there was no increase in organic sestonic phosphorus yet a phytoplankton pulse did occur. This could mean that the phytoplankton as a group absorbed very little, if any, of the phosphorus which was supposedly available to them at the overturn, even while they were increasing in number. Much interesting work has been done on the relationship of available phosphorus and *Asterionella*. Mackereth (1953) has shown that populations of *Asterionella* can grow in certain lakes containing as little phosphate phosphorus as one microgram per liter. Furthermore he found that they will continue to grow until there is only 0.06 micrograms of phosphorus per million cells. In other words even one microgram per liter of phosphorus is sufficient to support over 16 million cells per liter providing other nutrients, such as silicates, are not lacking. This concentration of cells is much greater than was ever found in Douglas Lake. Mackereth (*loc. cit.*) also has been able to demonstrate that *Asterionella*

can take phosphorus into store from media containing this element and partition it out to daughter cells down to a very low irreducible minimum, if the phosphate in the external medium becomes completely exhausted. This raises the whole question of how far phosphate is really a limiting factor in lakes and it would be of the greatest interest to know whether other algae including planktonic diatoms possess this property.

These facts help to explain how it could have been possible for the phytoplankton in Douglas Lake to increase in number without a simultaneous increase in organic sestonic phosphorus. The phytoplankton probably parcelled out their phosphorus content to daughter cells resulting in less phosphorus per individual cell but the same amount in the population as a whole.

This study provides no evidence that phosphorus is a limiting factor in the reproductive rate of phytoplankton in spite of the fact that phytoplankton pulses follow the overturns which supposedly distribute the bottom phosphorus throughout the lake (fig. 16). The present writer feels that because plankton pulses almost always occur immediately after the inception of an overturn, there is probably some cause-effect relationship. Perhaps during the overturn, certain other nutrients which may have a more profound influence on population growths are made available to the plankton.

The sequence of events which leads up to the development of a phytoplankton pulse is essentially as follows: Dead plankton organisms decompose at the bottom of the lake simultaneously with a decrease in oxygen in the hypolimnion. The nutrient elements which are liberated from the decomposing plankton, become tied up in ferric complexes in the bottom muds. As soon as oxygen is depleted from the bottom, these nutrients are liberated due to the reduction of the ferric complexes. These liberated nutrients are made available to the phytoplankton in the upper waters during the overturn.
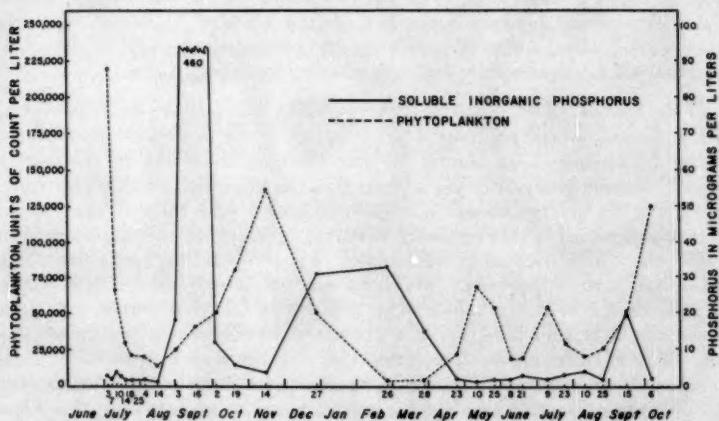
Fig. 16.—Seasonal variation of standing crop of total phytoplankton and soluble inorganic phosphorus at 20-meter depth in Douglas Lake. Years 1950-1951. See explanation of fig. 9.

It is hypothesized that the magnitude and duration of each of the phytoplankton pulses which occurs after an overturn may depend upon the magnitude and duration of nutrient liberation from the mud, which, in turn, depends upon how soon before the overturn the bottom becomes depleted of oxygen.

The question is raised regarding the factors involved in the production of phytoplankton pulses in shallow unprotected lakes having no outlets or inlets. The water in these lakes would presumably be in circulation most of the time and any thermal stratification occurring would be slight and of short duration. There would never be an oxygen depletion and hence no accumulation of nutrients at the bottom. The nutrients would probably be distributed uniformly most of the time. In a lake such as this it is probable that there would always be an adequate supply of nutrients available to the plankton. The productivity of phytoplankton in such a lake throughout the year should constantly be as great from the standpoint of nutrients as peak productions in thermally stratified lakes such as Douglas Lake. These small lakes, however, do show evidence of pulses, but according to Pennak (1949), the times of these pulses cannot be predicted. Also the number of pulses occurring in these lakes varies from lake to lake and from year to year in the same lake. If nutrients are not the limiting factor, then other factors must be involved. It is suggested that most of these factors do not stimulate the organisms to greater production but rather inhibit the production already in operation. These inhibitory factors might be the cause of the troughs in a graph depicting seasonal variations of phytoplankton populations in this type of lake.

SUMMARY

This investigation was undertaken to discover relationships which may exist between the seasonal and vertical distribution of phytoplankton and changes in physico-chemical conditions in five Michigan Lakes.

Plankton samples and physical chemical data were collected from Douglas Lake in northern Michigan during the summer of 1948 and during 16 consecutive months from July 3, 1950, and October 6, 1951. In addition, plankton samples and physico-chemical data were collected during the summers of 1948, 1950 and 1951 from Munro, Vincent and Lancaster lakes in northern Michigan and during the fall of 1950 from Lake Lansing in southern Michigan.

Morphometric data are presented. for each of the lakes. The four lakes in northern Michigan are only a few miles from each other, nevertheless, they differ markedly in their morphometric, physico-chemical and biological conditions.

The various fractions of phosphorus; soluble inorganic, soluble organic, organic sestonic and acid soluble sestonic are discussed. Methods for their determination and calculation are outlined.

Douglas is the largest of the five lakes studied. It shows typical thermal and chemical stratification with a gradual depletion of oxygen in the hypolimnion during the summer.

Munro Lake is shallow with no thermal or chemical stratification. It is second largest of the four northern lakes. Its chemical conditions resemble those of the epilimnion of Douglas Lake.

Lancaster Lake is deeper than Munro Lake but has a smaller area. It has a very marked thermal and chemical stratification during the summer. The epilimnion is very shallow and most of the volume of the lake is contained by the hypolimnion. The water in this lake is highly colored.

Douglas, Munro and Lancaster lakes are all slightly alkaline.

Vincent is a small shallow lake having soft water which is low in dissolved substances. It very seldom stratifies thermally. Its pH fluctuates but never varies greatly from 7.0. Comparison of these data with those of previous workers indicates that the water of this lake is gradually changing from acid to alkaline.

Lake Lansing in southern Michigan is a little smaller and deeper than Munro, however it has two depressions in which thermal stratification occurs. It is a hard water lake with the pH always on the alkaline side.

Concentration of total phosphorus in Munro Lake and in the epilimnial waters of Douglas and Lancaster lakes ranged between 6 and 13 micrograms per liter. In Vincent and in the epilimnion of Lake Lansing, the total phosphorus varied between 13 and 18 micrograms per liter, the latter two bodies of water containing more organic matter than any of the former three.

In the bottom waters of the hypolimnion of Douglas and Lancaster lakes, the phosphorus concentration increased tremendously soon after the oxygen had disappeared. In Douglas Lake, approximately two weeks after the inception of the overturn, the amount of phosphorus in the upper waters was no greater than before the overturn. This is contrary to what might be expected since it would seem that the stirring action in the water would have carried it to the surface.

Facts are presented to support the hypothesis that some of the accumulated phosphorus from the bottom waters actually was brought to the surface after the inception of the overturn but had disappeared before water samples were collected from the lake several days after the overturn had begun. Evidently, phosphorus reaching the upper waters can disappear in a matter of days because on September 16, 1950, the overturn had not yet begun and phosphorus was still concentrated in the lower waters of the hypolimnion, whereas 16 days later, complete vertical circulation was in progress and an increase in the phosphorus content of the upper water was not indicated.

Phosphorus at the bottom of the lake which is introduced into the upper waters at the time of the overturn is compared to artificial fertilizer added to a lake and the resulting chemical and biological conditions would be expected to be similar in both instances.

The chemistry pertaining to the release of phosphorus from the bottom muds to the overlying water is discussed. In the presence of oxygen, iron and phosphorus combine to form insoluble ferric complexes. When oxygen disappears from the bottom waters as a result of decomposition, the ferric complexes are reduced forming ferrous complexes which are soluble. When oxygen is reintroduced at the overturn, ferric complexes are once again formed.

During the 16-month period of investigation in Douglas Lake, the numbers of phytoplankton varied between 3,809 and 219,352 units per liter. Five separate pulses were observed; the first and second being the spring and fall pulses of 1950 occurring after the spring and fall overturn respectively, the

third and fourth making up a double spring pulse in 1951 and occurring after the spring overturn, the fifth representing the beginning of the fall pulse of 1951 following the fall overturn.

Douglas Lake is a diatom lake. Diatoms comprised an average of 76.2 percent of the entire phytoplankton production for the 16 months. The genera most abundant among the diatoms in each of the fall pulses were *Asterionella, Melosira* and *Synedra*, whereas the fall pulses contained mostly *Tabellaria, Melosira, Synedra* and *Fragilaria*. The Chrysophyceae represented exclusively by *Dinobryon* made up between 30 and 40 percent of each of the spring pulses. The other classes of algae together made up about 17 percent of the phytoplankton populations.

In Lancaster Lake, the summer standing crops never exceeded 42,791 units per liter. Chrysophyceae composed of *Synura* made up an average of 53.5 percent of the total. Diatoms were second, comprising 27.4 percent, whereas blue-greens and Dinophyceae were third and fourth contributing 30.5 and 28.6 percent respectively. Green algae were quantitatively insignificant.

During the summer months, Munro Lake contained phytoplankton crops in amounts ranging between 2,549 and 82,867 units per liter. Blue-greens were most abundant making up an average of 58.5 percent of the total. Diatoms produced 24.4 percent. Chrysophyceae contributed 14.4 percent whereas the Dinophyceae and green algae together amounted to about 6 percent.

During the summer months, the standing crops in Vincent Lake varied between 22,613 and 48,875 units per liter. Blue-greens were most numerous averaging 66.9 percent of the total. The Dinophyceae, composed only of *Peridinium*, contributed an average of 17.3 percent while the green algae made up 13.5 percent. Diatoms and Chrysophyceae together comprised about 2 percent.

The standing crops of phytoplankton in Lake Lansing during the fall of 1950 occurred in amounts ranging between 15,831 and 39,819 units per liter. These crops were composed mainly of diatoms, blue-green algae and Dinophyceae whose average contribution to the total were 51 percent, 34.4 percent and 13.7 percent respectively.

The average of the three mean summer standing crops for each of the northern lakes was computed. These averages show that Vincent produced the largest number of phytoplankton. Douglas Lake ranked second while Munro and Lancaster lakes came third and fourth.

Diatoms were the most dominant group in Douglas Lake whereas the Chrysophyceae made up the largest part of the population in Lancaster Lake. Blue-green algae were the dominant group both in Munro and Vincent lakes.

Green algae and Dinophyceae contributed the least to the populations of both Douglas and Munro lakes. Green algae were the smallest group in Lancaster whereas diatoms and Chrysophyceae were the least important groups in Vincent Lake.

In the four lakes, diatoms were most abundant in Douglas, next most numerous in Munro, less common in Lancaster and least numerous in Vincent. Green algae occurred most abundantly in Vincent Lake with Douglas, Munro and Lancaster following in order. Vincent Lake also produced the largest number of blue-greens with Munro, Douglas and Lancaster ranking second,

third and fourth. Dinophyceae appeared in greatest numbers in Vincent Lake followed by Douglas, Munro and Lancaster: the latter two lakes producing approximately equal numbers. The numbers of Chrysophyceae in Douglas and Lancaster lakes were approximately equal with Munro producing fewer and Vincent hardly any.

In comparing the mean fall standing crops of Douglas Lake and Lake Lansing, it was found that Douglas produced the larger population. Douglas Lake produced the larger number of diatoms whereas Lake Lansing produced the larger number of blue-greens and Dinophyceae. Neither lake produced many green algae or Chrysophyceae.

Discussions are presented of the individual genera of phytoplankton appearing in these lakes from the standpoint of their quantitative differences in the various lakes and at different times in the same lake.

There is no evidence in this study that the phosphorus liberated from the mud and brought to the surface waters during the overturn has any controlling influence over the reproductive rate of the phytoplankters in Douglas Lake probably because there is always a sufficient minimum present.

It is suggested that other nutrient elements which are combined with the ferric complexes and released at approximately the same time of the year as phosphorus, are responsible for the phytoplankton pulses occurring after each overturn.

The magnitude and duration of each of the phytoplankton pulses which occurs after an overturn may depend upon the magnitude and duration of nutrient liberation from the mud, which in turn depends upon how soon before the overturn the bottom becomes depleted of oxygen.

In shallow unprotected lakes which are undergoing almost constant circulation, there would probably always be an adequate supply of nutrients available to the plankton. Factors other than nutrients may control the formation of plankton pulses in these lakes. It is suggested that these factors do not stimulate the organisms to greater production but rather inhibit the production already in operation. These inhibitory factors might be the cause of the troughs in the graphs illustrating seasonal variation of phytoplankton populations in this type of lake.

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The Ecology of the Macroscopic Bottom Fauna in Lake Texoma (Denison Reservoir), Oklahoma and Texas

James E. Sublette

Northwestern State College, Natchitoches, Louisiana

With the advent of extensive flood control and hydroelectric projects, the field of limnology has had a new and imperfectly understood facet added in the form of numerous impoundments. While several studies have been made on smaller impoundments, few have been done on the larger and deeper ones of the Southwest. This is particularly true of studies of benthic organisms, as Greenbank's (1937) results from Elephant Butte Reservoir in New Mexico were the only ones suitable for comparison with the work presented here. Emphasis of this study has been on horizontal and vertical distribution and seasonal succession of the macroscopic bottom animals. A cursory examination of the other limnological features was also made (Sublette, 1955).

The major community which Klugh (1923) referred to as the lake bottom association has commonly been divided by limnologists into the littoral, sublittoral, and profundal zones. These zones are defined as follows: littoral, from the lake margin to a depth which marks the lakeward limits of the rooted aquatic vegetation; sublittoral, the area bounded by the littoral above and the profundal below; and profundal, roughly, the area of the bottom in contact with the hypolimnion. An examination of the literature shows the extreme variability of zones so described, not only between different bodies of water, but within a lake itself. This variability is primarily the result of two factors. One of these is the lakeward extension of rooted aquatic plants. It has been demonstrated (*vide* Welch, 1952) that different plant species have differing depth tolerances. Are two bodies of water, similar in every respect except that one has a shallow water and the other a deep water flora, to be considered as having entirely different littoral zones? The other variable factor is that of hypolimnion depth distribution. When a hypolimnion is present it varies in depth from season to season. Are the profundal zone limits then to change with the fluctuations of the hypolimnion? And what of the lake which rarely or never has a hypolimnion? Many writers, in order to avoid such poorly defined categories, have instead used the categories mentioned (littoral, sublittoral, and profundal) but have defined them by stating the exact depth limits of each zone. A more logical system would be to designate the zones on the basis of sediment substratum as has been pointed out by Pearse (1939) for marine communities.

The two major divisions, littoral and profundal, can readily be recognized as major communities since each exhibits a very different assemblage of organisms. What is not usually recognized is that within each major community ("zone") there are minor communities. Observations on these minor

communities (i.e., close agreement between bottom type, number of species and number of individuals) have been made by Baker (1918), Muttkowski (1918), Adamstone (1924), Rawson (1930), Krecker and Lancaster (1933), and Shelford and Boesel (1942). However, few of these workers recognized the components of each substratum type as a definite community and the results of those that did are not directly comparable because of lack of uniformity in terminology on bottom sediments and the associated communities.

The following is a classification of the major and minor communities as observed in Lake Texoma. The basic ecological terminology is that of Klugh (1923) with some additions. The classification of substratum is based on sediment terminology according to the Bureau of Soils Classification as modified by the U.S. Engineers Office, Ft. Peck, Mont., 1938 (vide Turnbull, 1945). Certain elements of Roelofs' (1944) hydrosols classification have also been incorporated.

Lake Bottom Association

    Littoral bottom (chilile systasis)—from 0 to 6 meters

        Gravel cenosis—gravel and sand greater than 70%, gravel predominates

        Sand cenosis—sand and gravel greater than 80%, sand predominates

        Emophyte cenosis—occurs within either gravel or sand cenosis (submerged aquatic vegetation)

        Clay consociation—occurs only as hardpan

    Ecotone—transition area between cenoses. The one between littoral and profundal cenoses (=sublittoral) shifts with seasons, local conditions; roughly corresponds to the 6 to 8 meter zone in Lake Texoma.

    Profundal bottom (mesophthmile systasis)—8 to 20 meters (maximum depth sampled)

        Mud cenosis—clay greater than 20%, organic content high chiefly as peat or muck.

APPARATUS AND METHODS

The study was made during June and July, 1949, and from June, 1950 to May, 1951. The first two months study was a preliminary survey of the fauna of the lake as sampled at random at eight areas of the lake: Rock

Creek, Newberry Creek; Big Glasses Creek; Cold Spring Creek; Hickory Creek; Buncombe Creek; the Islands; and Caney Creek. This survey is the source of most of the horizontal and vertical distribution of the benthos. The second period of the study, June, 1950-May, 1951, was concerned with securing data on seasonal succession of the benthos.

A six-inch square Ekman dredge was used as a bottom sampler, except for six samples taken with a nine inch square Ekman dredge. During the preliminary survey one dredging constituted a sample; during the seasonal study, four dredgings in the littoral and three in the profundal constituted a sample. A total of 350 dredgings making up 158 samples was taken.

Several sampling methods were employed to study the faunal distribution caused mainly by the inefficient functioning of the Ekman dredge in many situations. In shallow water with a fine sand or sand-silt bottom the Ekman was hand operated (forced into the substratum by hand instead of being lowered by a rope). In other places in the upper littoral, qualitative sampling was done with a heavy duty, fine mesh, aquatic dip net. Such samples were supplemented with those taken with a six foot fry seine which secured many motile forms that could not otherwise be taken. The details of sampling procedure have been presented in an earlier paper (Sublette, 1955) and will not be repeated here.

AUTECOLOGY

PORIFERA

Spongilla lacustris (Linné).—This sponge was taken once, December 8, 1950, on a rocky headland shore east of the University of Oklahoma Biological Station. The habitat was a ledge of limestone bed rock overlain with boulders, gravel, and some sand and silt normally under several feet of water but at the time was just awash because of low water level. The area is subjected to slight wave action as evidenced by the accumulation of sand and silt in the interstices of the gravel-boulder ledge. The individual sponges were rather small and were abundantly distributed over most of the ledge. The habit of this species is incrusting; the coloration brown with a faint greenish tinge, probably caused by the large number of diatoms found living among the cells.

Asteromeromeyenia radiospiculata (Mills).—This sponge was collected by W. J. Harman of Louisiana Polytechnic Institute on submerged timbers of the boat house of the University of Oklahoma Biological Station, July, 1954. One specimen, roughly oval in outline, was low mound-shaped and measured approximately four centimeters by one centimeter. Dr. Minna E. Jewell, who determined the species, stated that there were a few flesh spicules of *Spongilla lacustris* included with the material of *A. radiospiculata*. This may be an indication of a much wider dispersal in the lake for *S. lacustris* than was found during the original study period, 1949-1951.

NEMATODA

On several occasions small free living nematodes were recovered from the samples. No attempt was made to determine species. No apparent depth or sediment preference was found.

BRYOZOA

Plumatella repens Linné.—This bryozoan flourished in several situations in the reservoir and was common on the undersides of floating leaves of *Potamogeton americanus*, on submerged sticks and logs, and along rocky shores which were subjected to little or no wave action. The colonies varied in size from less than one centimeter to a maximum of more than five centimeters. Statoblasts averaged a dimension ratio of one to three. Colonies consisted almost entirely of repent branches and were collected from late in June until the middle of December.

ANNELIDA

OLIGOCHAETA

Because of methods of collection and preservation, annelids collected were in poor condition for specific identification.

The group showed a decided preference for soft bottoms composed of mud or silty sand, and were dredged from practically all depths throughout the year. The distribution of Oligochaeta showed a bimodal curve when numbers were plotted against depth. One peak occurred in the littoral and the other in the profundal; the distributional pattern probably was caused by different species having different depth tolerances.

HIRUDINEA

One small undetermined specimen of a leech was taken during the investigation. This was at Rock Creek (Station I) in seven meters of water on a mud bottom.

MOLLUSCA

PELYCEPODA

Freshwater mussels were rather sparsely represented in Lake Texoma by five species: *Quadrula q. apiculata* (Say), *Truncilla donaciformis* (Lea), *Leptodea laevissima* (Lea), *Anodonta corpulenta* (Cooper), and *A. imbecillis* (Say). *Leptodea laevissima* was the most prevalent species probably due to its ability to migrate with fluctuating water levels as described by Isely (1924). Collections at periods of extremely low water levels rarely yielded living specimens of *L. laevissima* and then only in deep pockets left by the receding waters, but the relative dominance in numbers of this species over other pelecypods was clearly indicated by the number of shells found along the shore line. The empty shells probably resulted from normal mortality within the population at high water levels.

All five species were collected in the shallow, protected inlets and bays in the sand cenosis. The exact limits in depth are not known, but were probably from one to six meters. Beyond this depth the amount of sand in the substratum decreased to a point where the bottom will no longer support the weight of a mussel. There was no indication of a shell zone. Compared with other bodies of water Texoma was a poor mussel lake, possibly because of wide seasonal fluctuation of water levels.

Dr. Henry Van der Schalie, University of Michigan, determined the species of Pelecypoda.

GASTROPODA

Three species of Gastropoda, *Physa halei* Lea, *Lymnaea* (=*Fossaria*) *modicella* (Say), and *Ancylus* sp. were found in the lake. Determination of the first two species was made by Mr. R. Tucker Abbott, formerly of the U.S. National Museum, now at the Academy of Natural Sciences, Philadelphia.

The only specimens of *L. modicella* collected were taken while seining the recently overflowed margins of the lake near the border of a permanent marsh. This is in agreement with Baker's (1928) statement that this species does not normally live in large bodies of water but prefers mud flats or small pools. It seems likely that the species is not usually found in Lake Texoma.

Physa halei was widely distributed in the lake. Specimens were collected in a variety of situations including gravel substratum with moderate wave action; sand substratum with much debris and little wave action; and on *Potamogeton americanus*. Most individuals were collected on clumps of *Potamogeton*.

Several specimens of an undetermined species of *Ancylus* were collected along with *Physa halei* on *Potamogeton*.

ARTHROPODA
CRUSTACEA
PALAEMONIDAE

Palaemonetes (*Palaemonetes*) *paludosus* (Gibbes).—This freshwater prawn was typically collected in the *Potamogeton* beds in Texoma although it occurred also among debris along the shore. Creaser and Ortenburger (1933) characterized this prawn as an inhabitant of slowly moving streams and ponds periodically overflown by rivers. These habitat preferences were reflected by its distribution in the reservoir, where it was taken only in well protected bays and inlets which were subjected to little or no wave action. It was a normal component of the emophyte cenosis and did not occur in dredgings. Ovigerous females were taken in June and July.

ARGULIDAE

Argulus lepidostei (Kellicott).—The presence of an argulid in bottom samples is of interest since normally it is an ectoparasite of fish. One specimen of this species was taken on a gravel shore in approximately one and one-half meters of water on the east side of Buncombe Creek Bay on September 6, 1950.

ARCHNOIDEA
HYDRACARINA

Since the water mites were represented in Lake Texoma by few individuals no attempt was made to determine them to species. The group was restricted to the places in the littoral having firm gravel or sand bottoms. The greatest concentration of individuals occurred near the deeper portion

of the depth range. A peak in number of individuals (42 per square meter) occurred in late fall (October 23) with a population minimum occurring in summer.

INSECTA

EPHEMEROPTERA

The following species of mayflies were collected: *Caenis* sp., *Brachycercus lacustris* (Needham), *Stenonema femoratum tripunctatum* Banks, *Callibaetis montanus* Eaton?, *Siphlonurus* sp., *Hexagenia munda elegans* Traver, and *H. limbata venusta* Eaton. Dr. Lewis Berner of the University of Florida determined the species of *Hexagenia*.

The mayfly fauna was distinctly divided into two components, the mudburrowing forms (*H. munda elegans* and *H. limbata venusta*) and the firm bottom (including *Potamogeton americanus*) inhabitants.

The two species of *Hexagenia* were very distinct as adults, *H. munda elegans* being larger with reddish-brown to black coloration and *H. limbata venusta* smaller with a creamy yellow coloration. The immature stages were not so distinct although there was a size difference. The mature naiad of *H. munda elegans* was definitely larger. However, since many collections consisted of mature and immature specimens, producing a size range overlap between the two species, size was not a useful taxonomic criterion. It was found that the most reliable taxonomic characteristic was the coloration of the imago which showed through the thin cuticula of the naiad. Length and shape of frontal prominence as well as length of mandibles, extent of mandibular cross over, and various head ratios were found to be of little value in separating these species in the earlier instars. The shape of the frontal prominence was diagnostic, however, in naiads approaching maturity (Spieth, 1941).

Hexagenia munda elegans Traver.—*H. munda elegans* was more common than *H. limbata venusta* both in naiad and adult collections. In Lake Texoma its distribution was chiefly profundal, although considerable numbers occurred in the lower littoral area. The population maximum was near the eight meter contour on the lake bottom with gradually diminishing numbers both shoreward and lakeward. As Lyman (1943) has demonstrated *Hexagenia* naiads are sensitive to decreasing amounts of oxygen and are intolerant of sediments with high sand content. The distribution of *H. munda elegans* was, therefore, a normal one in that the organisms were seemingly located in response to these two factors.

The seasonal distribution for *H. munda elegans* was typical of many benthic organisms. The period of adult emergence was from late May to August. At this time the number of naiads was at its lowest point. The numbers appearing in the dredgings increased from the summer minimum to a maximum in February. The maximum number recorded was 625 per square meter on February 10, 1951. Following this, there was a gradual decline until the population minimum was reached in midsummer.

Hexagenia limbata venusta Eaton.—This species differed little from the preceding in ecological characteristics. It was not nearly as numerous nor as tolerant to depth since the maximum numbers (32 per square meter, February

10) occurred near the six meter contour. Its seasonal history was similar in every respect except that the season of emergence was about two weeks later than of *H. munda elegans* and apparently lasts slightly longer.

There has been some question as to the validity of the subspecies *H. limbata venusta*. Spieth (1941) divided *H. limbata* into five subspecies which he maintained were distinct although interbreeding where overlap occurs. He says, "for all of these subspecies intergrading specimens of geographically adjoining subspecies have been found." Hunt (1951) says that this species is extremely variable as to color phases with all phases freely interbreeding. He therefore dismissed Spieth's subspecies as invalid. It would appear that Spieth's subspecies could be accepted if at any one geographic location the subspecies remained constant, that is, without variation in the subspecific characteristic (in this case, coloration). Since this apparently was the case at Texoma, the author feels justified in retaining the subspecies *H. limbata venusta*.

Caenis sp.—The naiad of this small two-winged mayfly was the most characteristic inhabitant of the littoral zone. It occurred in all littoral cenoses except bare sand. It was not numerous and contributed little to the community. *Caenis* exhibited a normal seasonal distribution with maximum numbers (21 per square meter) in midwinter and a minimum in summer.

Brachycercus lacustris Needham.—The sprawling naiad of this mayfly was collected only four times during the study from the littoral bottom on silty sand or gravelly sand. Adults were not associated.

Stenonema femoratum tripunctatum Banks.—Literature records for Oklahoma have included the species *S. tripunctatum* and *S. birdi* Traver. According to Spieth (1947), these are not valid species but only color phases of the subspecies *S. femoratum tripunctatum*. Although both forms of *Stenonema* occurred in Lake Texoma, they are considered here as one. It was one of the characteristic lentic benthic forms and was found in the rapids of all clear gravel bottom tributary streams examined. Its location in a lotic cenosis can be attributed to the gravel cenosis in Lake Texoma duplicating, at least partially, the conditions in a stream. Specimens were collected on three dates at three different rocky promontories. Adults were not taken.

Callibaetis montanus Eaton?.—Naiads were collected on two occasions in the upper sand (silty sand) cenosis. *C. montanus?* appeared to prefer very quiet waters, having been collected in well protected, deep inlets. Adults were collected in July.

Siphlonurus sp.—An undetermined species of *Siphlonurus* was collected on two occasions from the same cenosis as *Callibaetis montanus?*. Adults were not collected.

ODONATA

Suborder ANISOPTERA

Pantala hymenea Say, *Erpetogomphus* sp., and *Gomphus plagiatus* Selys were the dragonflies collected. Dr. George H. Bick, Tulane University, deter-

mined the first two species listed. The specific placement of *G. plagiatus* is after Garman (1927).

Pantala hymenea Say.—The naiad of this species was taken only twice, both times in water of about a meter in depth on a sand bottom overlayed with much debris. Adults were collected on August 11, 1950.

Erpetogomphus sp.—Naiads were collected only from the littoral zone in the sand cenosis, in water less than three meters deep. It was the most common dragonfly in the benthic communities.

Gomphus plagiatus Selys.—This species, collected only once, occurred on a sand bottom at three meters. Adults were not taken.

Suborder ZYGOPTERA

Enallagma civile (Hagen).—Naiads were apparently confined to sand bottoms. Specimens were collected by dip net only. Adults were not collected.

Ischnura sp.—This form showed the least preference for substratum type. The collections were as follows: sand (2), gravel (1), and *Potamogeton americanus* (1). Species of this genus recorded from the Red River drainage are *I. denticollis* Bur., *I. posita* Hagen, *I. kellicotti* Williamson, and *I. verticalis* Say (Bird, 1932).

Argia moesta (Hagen)?.—This species was one of the most characteristic benthic inhabitants of the gravel cenosis, being found in no other situation. Like *S. femoratum tripunctatus*, this form was apparently a typical stream form that was able to survive in this cenosis because of the duplication of the environment of the normal habitat. Adults were collected: February 10, July 12 and 31, 1950.

Argia spp.—Several specimens differing from *A. moesta*? were collected, most of them from the gravel cenosis.

TRICHOPTERA

The following caddis flies were collected: *Cyrnellus marginalis* (Banks), *Oecetis inconspicua* (Walker), *O. cinerascens* (Hagen), *Hydroptila* sp., and *Orthotrichia* sp. Dr. H. H. Ross of the Illinois Natural History Survey examined all but the last two species listed.

Cyrnellus marginalis (Banks).—This species, along with *Oecetis inconspicua* (Walker), was collected in considerable numbers in the light traps. In larval collections two species were prevalent, *Oecetis inconspicua* and a previously undescribed psychomyiid larva. Since the only adult species of Psychomyiidae collected was *C. marginalis,* this larva is described by supposition as *C. marginalis.*

Mature larva: This larva will key to couplet 5, page 53 of Ross' (1944) key to the Psychomyiidae. It differs from Genus A as described by Ross on the basis of mandibular pattern.

Cyrnellus marginalis showed a decided preference for a firm bottom substratum, being most frequently found in the gravel or sand (gravelly sand) cenoses. It occurred occasionally on *Potamogeton americanus* and clay hardpan shoals. It was a littoral form being found at a maximum depth of four meters. Maximum numbers (172 per square meter) were dredged on October 23 with a gradual decline in numbers until late spring, when emergence occurred. Adults were collected from June to September.

Oecetis inconspicua (Walker).—Like *Cyrnellus marginalis*, this caddis fly was a littoral form. Its substratum preference was slightly different, however, with individuals most frequently occurring on a sand substratum and only rarely on *Potamogeton* and gravel. Individuals were collected in depths as great as nine meters, indicating a greater depth tolerance than *C. marginalis*. Maximum numbers (21 per square meter) occurred on November 12.

Oecetis cinerascens (Hagen).—This caddis fly, easily identified in the field by means of its log-cabin type of case, occurred in Texoma only among clumps of *Potamogeton*. Specimens were collected only at one site. Adults were not collected.

DIPTERA
CULICIDAE
Subfamily CHAOBORINAE

The distribution of *Chaoborus punctipennis* in Lake Texoma agreed in every particular with the results found by investigators of natural lakes (Muttkowski, 1918; Juday, 1921, 1922; Eggleton, 1932). It was the most typical profundal benthic organism in Texoma, being restricted to the soft sediments of deep water. When numbers are plotted against depth, *Chaoborus* shows a sloping curve with minimal numbers occurring in the littoral and maximal in the profundal regions. Numerically, it was the predominant benthic organism making up roughly fifty percent of summer standing crop. Its seasonal numerical dominance is graphically shown in fig. 1, in which the number of *C. punctipennis* are plotted with the total number of organisms.

TABANIDAE

Chrysops sp. and *Tabanus* sp.—Horsefly larvae were collected only upon one occasion, while seining along the recently inundated shore in the vicinity of a marsh. It is improbable that these species were normal inhabitants of the lake. Adults were not associated.

STRATIOMYIIDAE

Stratiomyia sp.—Only one soldier-fly was collected, along with the Tabanidae. Adults were not associated.

EPHYDRIDAE

Hydrellia sp. — The one shore-fly larva represented in Texoma by only one species was restricted to the *Potamogeton* (emophyte) cenosis. Adults were not associated.

HELEIDAE

Culicoides was the only genus identified from the material collected. Since the immature stages are imperfectly known no further taxonomic treatment was considered.

Members of this family were found in practically all substratum types and depths, although a maximum number occurred at eight meters with gradually diminishing numbers lakeward and shoreward.

Although this group was insignificant in numbers of individuals, it is probably important in the ecology of the benthic assemblages because of the predaceous habits of the larvae. Quantitative results indicated little seasonal variation in the number of larvae. A slight peak was reached on November 12 (48 larvae per square meter) with only slightly lowered numbers for the remainder of the year. Adults were not separated from the light trap material.

TENDIPEDIDAE

Subfamily PELOPIINAE

Pentaneura basalis (Walley)?.—An examination of the adult tendipedid fauna over a ten months period revealed two species of *Pentaneura* present, *P. annulata* (Say) and the species referred to as *P. basalis* (Walley)? by Johannsen (1946). The bottom fauna collection disclosed two distinct larval types, one of which is *P. annulata* (as described by Malloch, 1915) and the other a form which the writer associated with *P. basalis?*. This latter form has been briefly described by Malloch as *Tanypus* sp. A. The two species may be separated on the basis of a difference in lingula patterns (Malloch, 1915, Plate XXV, figures 2 and 7) and a difference in mandibles. The mandible of *P. basalis?* is much more strongly hooked, the tip being at right angles to the base; the auxiliary tooth is prominent in *P. annulata* while it is indistinct or absent in *P. basalis?*.
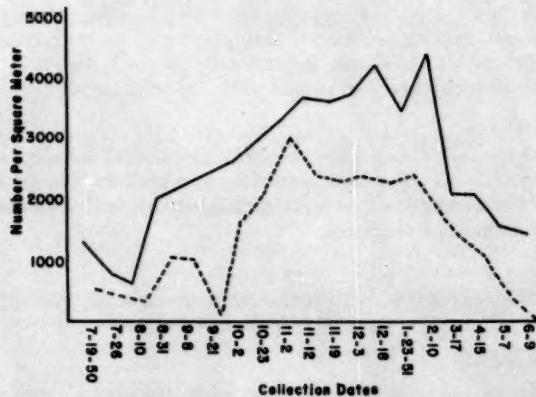
Fig. 1.—Annual standing crop of bottom organisms (solid line) showing numerical dominance of *Chaoborus punctipennis* (dash line).
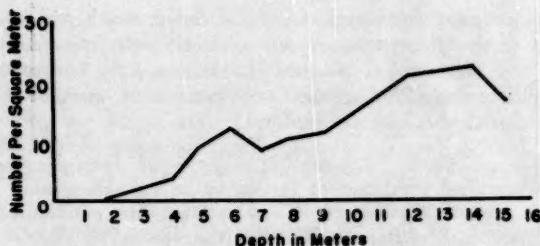
Fig. 2.—The depth distribution of *Pentaneura basalis?* as shown by a smoothed curve of the summer population (June, July, 1949).

The pupa of *P. annulata* was not distinguished from that of *P. basalis?*. The larvae of the Pelopiinae are not tubicolous as are most Tendipedidae. Instead they are predacious, feeding largely upon other Tendipedidae and smaller aquatic animals (Johannsen, 1937). This predatory habit is reflected in the horizontal distribution of *P. basalis?*. Specimens were collected on all cenoses beyond two meters with the greatest concentration in deep water. The distribution trend is shown in fig. 2. According to quantitative results, this form was predominantely profundal. The distribution into the littoral bottom is explainable on the basis of its predatory habits. The seasonal maximum was reached on February 10 with 27 organisms per square meter recorded. Adults were collected from May 7 to September 1.

Pentaneura annulata (Say).—The immature stages of this species were described as *Pentaneura monilis* (Malloch, 1915, not Linné). The specimens collected agreed in all details with Malloch's description.

Larvae of *P. annulata*, while similar in feeding habits to *P. basalis?*, were distinctly littoral forms, occurring in all littoral cenoses to a depth of six meters. A maximum number of individuals was found at two meters, occurring with less frequency than *P. basalis?*. The relatively few individuals collected made accurate seasonal fluctuations impossible to determine. Probably it agreed with the majority of the tendipedids in having a midwinter maximum and a summer minimum. Adults were collected from April 15 to September 1.

Pelopia stellata Coq.—The characteristics of this larva agreed with those given by Johannsen (1937). The habitat preference was the same as *Pentaneura basalis?*. *P. stellata* was found in much larger numbers, being the most prevalent profundal tendipedid and the second most prevalent benthic organism. The seasonal distribution of the larvae was most unusual, with maximum and minimum numbers occurring in reverse to most tendipedids. The maximum numbers collected (1625 organisms per square meter) was on September 29. The population was smallest in late winter and early spring. Adults were collected from March 17 to November 19.

Procladius bellus (Loew).—The larva has been described by Malloch (1915) and Johannsen (1937). It was a member of the profundal assemblage,

having been collected from three to fifteen meters depth with a maximum occurring at about eight meters. *P. bellus* was a poorly represented predatory tendipedid with an atypical seasonal distribution. A seasonal maximum occurred in the spring (590 organisms per square meter on April 18). Adults were collected from April 15 to October 23.

Procladius culiciformis (Linné).—The larva of *Procladius culiciformis* was not distinguished from that of *Procladius bellus*. Since adult specimens of *P. bellus* were most common, it was assumed that practically all larval specimens were of the latter species. For this reason, all *Procladius* larvae collected were included under *P. bellus*. This contention was further strengthened by Morrissey's (1950) work in Iowa where he found *P. culiciformis* emerging from clumps of aquatic vegetation. The absence of distinguishable *P. culiciformis* larvae could then be explained on the basis of a sparse population and a cursory examination of the emophyte cenosis. Adults were collected from April 15 to June 9.

Coelotanypus.—Three species of *Coelotanypus* were collected as adults in the light traps: *C. tricolor* (Loew), *C. concinnus* (Coq.), and *scapularis* (Loew). While three species of adults were collected, only one larval form could be distinguished, that of *C. concinnus*, the only species described in the larval stage. Presumably the other two species were present as larvae but were indistinguishable from *C. concinnus*. These three morphologically indistinguishable species presumably had slightly different substratum preferences as shown when numbers of *Coelotanypus* spp. were plotted against depth. The resulting curve was a trimodal one with one small peak at one meter, a much larger one at eight meters, and still another, slightly smaller, at fifteen meters. The seasonal distribution as sampled in the mud cenosis was a normal one with a seasonal maximum of 625 individuals per square meter on February 10. The minimum for this substratum occurred in July.

Adults of *C. tricolor* were collected from July 6 to September 1; those of *C. scapularis* from February 2 to September 22; and *C. concinnus* from July 6 to September 22.

Subfamily HYDROBAENINAE

Hydrobaenus (Psectrocladius) sp.—This previously undescribed larva most closely resembles *H. (P.)* sp. *a* Roback (1953a). The larva is characterized thus: The length is 4 mm. Only the tips of the mandibles and labium are brown, the rest of the head and body is light yellow. The eyespots are contiguous, the smaller being only one-third the diameter of the larger one. Antennal ratio, 36:14:2:1:1; the blade reaches the base of the third segment. The labrum appears glabrous; the epipharyngeal area is margined with several blade-like bristles. The mandibles are slender and rather straight. The accessory tooth and bristles appear to be absent. The labial plate is strongly arched so that the lateral teeth appear only on a depressed plate. The plate bears 12 teeth, 5 dark laterals on each side, a median colorless area (fig. 20, Roback, 1953a) is very similar. The posterior prolegs bear a series of dark brown retractile claws. The preanal papillae are only slightly

longer than wide, distinctly dark brown and apparently scleritized. On the specimens studied the papillae bear only one terminal bristle.

The pupa and adult were unassociated.

This species was another of the littoral assemblage occurring from the water's edge to a depth of seven meters. There was little evidence to indicate a substratum preference since specimens were collected in sand, gravel, and emophyte cenoses. Paucity of individuals prohibited a discussion of seasonal distribution.

Hydrobaenus (Hydrobaenus) sp.—This previously undescribed larva is apparently most closely related to the species figured by Roback (1953a) as *H. (H.)* sp. *b*. Larva: The body is 3 to 4 mm in length with a greenish coloration. The head is yellowish with only the lateral teeth of the labial plate and the tips of the mandibles brown. The antennae are very short, five segmented, and about half the length of the mandibles; the segments bear to one another the ratio 20:8:5:10:6; the blade exceeds the apex by a distance equal to the length of the last antennal segment. Details of the labral and epipharyngeal areas could not be distinguished on the specimens at hand. The mandible is slender and rather acutely tipped with three dark teeth; the accessory tooth is apparently absent; a mandibular brush is present, composed of several basally fused rays. The labial plate has 11 teeth, the central one broadly rounded and colorless (fig. 16-B—Roback, 1953a). A paralabial beard may be present but could not be seen with certainty. The preanal papillae are about 1½ times as long as broad, each bearing 7 bristles. The posterior prolegs are very short, the claws appearing to arise from the segment itself. The claws are about 24 on each leg, all are yellowish and apparently oriented in the same plane. The anal gills are 4 in number; the dorsal pair are widely separated and conspicuous, the ventral pair very short, close together, and inconspicuous. The gills are tapered broadly and are rounded. The dorsal pair are as long as the preanal papillae; the ventral pair are about half as long.

The adults and pupa were unassociated.

This larva was collected only on one date, May 7, 1951, from the gravel cenosis of the littoral bottom. Since mature larvae were collected, it is probable that emergence took place shortly after this date.

Hydrobaenus (Smittia) sp.—In the absence of associated adults, the subgeneric placement was based on Johannsen's (1937) description of *Hydrobaenus (Smittia)* sp. E, Group *Epoicocladius* Zavrel. Malloch (1915) briefly described this larva as genus *Incertus* B. Roback (1953b) has illustrated a labial plate of a species designated as *H. (S.) ephemerae* (Kief.). The larva described as follows may be identical. Mature larva: The length is 4.5 to 5 mm. The body has a greenish cast. The antennae are slightly longer than the mandibles. The antennal ratio is 14:4:1:1:1; the blade exceeds the tip of the antenna by a distance equal to the last three segments. The eyes are roughly reniform. The maxillary palp is short with the basal segment ringlike. The labial plate is strongly arched with the lateral margins black, the central area colorless, a strong bristle at each posterior-lateral angle. (See Malloch, Plate XXIX, fig. 23.) These lateral black margins were irregular,

possibly indicating lateral teeth; however, none could be seen with certainty on the specimen at hand. The body segments are very distinct, each bearing 4 strong bristles and 2 to 6 finer, less distinct bristles. The preanal papillae are slightly more than 1½ times as long as broad. Each papilla bears 7 strong terminal bristles with an additional shorter bristle located on the anterior median aspect of the papilla. The 2 anal gills are long and tapering to a point. Each gill is basally constricted. The posterior prolegs are long with brown retractile claws.

The pupa and adult were unassociated.

Hydrobaenus (*Smittia*) sp. was always found in littoral sediments with a slight overlap into the profundal as defined herein. Specimens were collected from three to eight meters. This distribution was coextensive with that of *Hexagenia limbata venusta*. Although *Hydrobaenus* (*Smittia*) sp. was not collected on *Hexagenia limbata venusta*, there is a possibility that it was a commensal (or ectoparasite) on that form having been dislodged during screening. The species which most closely resembles *Hydrobaenus* (*Smittia*) sp. was described by Johannsen (1937) as *Hydrobanus* (*Smittia*) sp. E. This sp. E of Johannsen was found clinging to the legs and gills of *Hexagenia recurvata*. Johannsen's placement was based on *Hexagenia ephemerae* which was described by Sulc and Zavrel (1924) as a symbiont on *Ephemera vulgata*.

Hydrobaenus (*Eukiefferiella*) sp.—This previously undescribed larva belongs to the subgenus *Eukiefferiella* as restricted by Johannsen (1937). One adult male, in poor condition, was identified for this genus.

Mature larva: The length is 3.5 to 4.5 mm. The body is yellowish-green. The head, which is slightly tapered anteriorly, is light yellow except for the occipital margin, the tips of the mandible, and the 4 lateral teeth of the labial plate which are dark. The antennal ratio is 16:5:2:1:1; the blade reaches the apex of the 4th joint. The antennae are only slightly more than half as long as the mandibles. The labrum has a pair of bristles on the dorso-anterior margin; a pair of small forked bristles, and a group of small pointed blades on the ventro-anterior margin. The epipharyngeal area bears 10 to 12 curved blades, a pair of which appear bifid at the tip. The mandibles are brownish with the teeth black; the inner basal portion is practically colorless and bears the 3 to 4 serrations characteristic of the subgenus. The labial plate has 13 teeth; the lateral 4 on each side are dark. The central tooth is about 4 times the first laterals in width, and in mature larvae, slightly shorter. The anterior eye spot is about half the size of the posterior and is separated from it by a distance less than a third its own diameter. The preanal papillae are small, about as long as wide; each bears 5 bristles. There are 4 anal gills; the dorsal pair is one third longer and broader than the ventral. Posterior prolegs are about as long as the dorsal pair of gills; each leg has about 20 yellowish-brown claws.

The pupa and adult were unassociated.

H. (*Eukiefferiella*) sp. was another of the littoral assemblage. Individuals were collected from zero to six meters only on gravel and sand substrata.

Cricotopus tricinctus (Meig.).—The larvae of this genus that were collected keyed in Johannsen (1937) to *C. trifasciatus* (Panzer). Johannsen states that *C. tricinctus* cannot be distinguished from *C. trifasciatus* in the

larval and pupal stages. As *C. tricinctus* was the only adult of the genus collected at Texoma, this larva was associated with it.

This species was most frequently collected as larvae on *Potamogeton;* however, it was collected not too infrequently on other substrata, namely, gravel, and clay hardpan. It was taken only in the littoral zone on these substrata.

Adults were collected from April 15 to November 2.

Subfamily TENDIPEDINAE
Tribe CALOPSECTRINI

Calopsectra (Calopsectra) neoflavellus (Malloch).—The larva and pupa of this species have been briefly described by Hauber (1944) as *Calopsectra (Calopsectra)* sp. B. The dead pupa from which the description was drawn contained the male hypopygium which was in poor condition. Associated material (mature pupae with clearly distinguishable hypopygia) was collected on several occasions in Lake Texoma indicating the affinities of the stages. The following description is given to supplement Hauber's description.

Mature larvae: The length is 3 to 3.5 mm. The color is yellowish brown; head, pale yellow except the mandibular teeth and the teeth of the labial plate. The antennal socket is elevated, with the inner side bearing a low tubercle but without a spine. The antennae are elongate; ratio, 36:6:4:5:2. The Lauterborn organs are extremely long-petiolate, 2 times the 3 distal antennal segments. The labial plate is 11-toothed; the middle tooth, which is trilobed, is rather broad and variable depending on age and amount of abrasion. The paralabial plates are separated on the midline by a distance less than 1/3 the width of the central tooth. The posterior prolegs are short; the claws massive with a yellowish coloration. There are 2 anal gills which are slightly shorter than the preanal papillae. Preanal papillae are robust, longer than wide; each bears 6 strong, dark brown bristles. The larva inhabits a tube constructed from sand grains.

Pupa: The respiratory organs are very similar to fig. 24 of Hauber (1944). The frontal tubercle is long and conical with an apical bristle. The comb of the 8th segment has 7 large sharp marginal teeth with a variable number of shorter teeth on the disk, usually around 10 in the specimens examined. Hauber (1944) gives a number of 16 to 20 for these.

Adult: These are as described by Malloch (1915), Hauber (1944), and Johannsen and Townes (1952).

Calopsectra neoflavellus was another of the tendipedid fauna restricted to the littoral zone. It occurred principally in the sand cenosis. A maximum number of larvae (155 per square meter) was collected on April 15.

Adults were collected from April 4 to September 1.

Calopsectra (Calopsectra) dissimilis (Joh.).—The immature stages of *C. dissimilis* are as described by Johannsen (1937). The ecology of the species was very similar to that of *Calopsectra neoflavellus* except that it exhibited a much greater latitude of substratum preferences. It normally occurred in the sand cenosis but was also taken in gravel and *Potamogeton*. A maximum number of 75 per square meter was found on January 23.

Adults were collected from July 6 to October 10.

Calopsectra (Stempellina) bausei (Kieffer)?.—The immature stages agreed in every detail with the description given by Johannsen (1937). This tendipedid was taken only in the littoral zone in the sand cenosis.

Tribe TENDIPEDINI

Pseudochironomus pseudoviridis (Malloch).—The adult specimens of this species agreed with the description given by Townes (1945) for a variant from Lugert, Oklahoma, in that the ventral appendages of the hypopygium were divided slightly over halfway to the base. Since only one species of this genus was collected at Texoma in the adult stage, the larva described below as new is assumed to be associated with this species.

Larva: The generic placement is based on Hauber's (1947) description of *P. fulviventris* (Joh.). In describing this species as new he overlooked Johannsen's (1937) description of *Tanytarsus* [=*Pseudochironomus*] (sens. lat.) sp. J. This sp. J is unmistakably a member of the genus if not the species described.

The larva herein associated as *P. pseudoviridis* is similar in almost every respect to *P.* sp. J (Joh.) and *P. fulviventris* (Joh.) Hauber. The length is 5 mm. The antennal ratio is 16:5:3:3:1. The blade extends to the tip of the 4th segment. The mandible is long and heavy; the inner margin with 4 uniformly dark teeth, of which the basal one appears to be fused with the mesio-proximal shelf of the mandible. The labial plate and other features are as in *Pseudochironomus* sp. J. (Joh.) and *P. fulviventris* (Joh.) Hauber.

Pupa: One cast skin which is probably associated with this species was found at the water's edge. The skin was 6 mm long and practically colorless. A prominent cephalic tubercle with a long preapical bristle was present. Respiratory organs could not be seen, so presumably they were lost. The lateral margins of segments 7 and 8 bore 4 bristles. The caudo-lateral angle the 8th segment was broadly rounded and supported 10 broadbased spines. The swim fin had about 40 bristles.

The larvae of *P. pseudoviridis* were characteristic of the upper littoral, being found in water less than three meters in depth. The largest number of individuals occurred on silty sand, but specimens were also collected from gravelly sand and gravel. This species was poorly represented in the dredgings but sufficient numbers of larvae were collected to indicate that a maximum (21 per square meter) occurred around December 18, with a minimum occurring in midsummer.

Adults were collected from July 6 to August 29.

Polypedilum (Tripodura) digitifer Townes.—Adult specimens of two species in the genus *Polypedilum* were collected at Texoma, *P. (T.) digitifer* Townes and *P. illinoense* (Malloch). Adults were collected in a ratio of about forty *P. digitifer* to one *P. illinoense*. Upon examining the larval material, only one apparent larval type was encountered; this appeared to be *P. illinoense*. Later in the investigation, two mature pupae were collected with attached larval skins. These pupae were clearly *P. digitifer* (as evidenced by the visible male genitalia in the cleared specimen) although the larval exuviae resembled the *P. illinoense* type. Although these larvae are superficially identical with *P. illinoense*, one is led to infer that they are actually

P. digitifer. This contention is further strengthened by the work of Berg (1950), who found the larvae of *P.* (*P.*) *illinoense* living in *Potamogeton natans.*

In Lake Texoma most of these *P. illinoense* type larvae were collected from the lake bottom, not on *Potamogeton.* This would indicate a different species. The paucity of larvae on *Potamogeton* is a reflection of the population density of adults.

A critical examination of the Texoma material of *P. digitifer* showed these differences when compared to the descriptions of the larvae of *P. illinoense* as given by Hauber (1947) and Berg (1950).[1] The antennal ratio is 14:6:1:3:1 as compared to Hauber's ratio (for *P. illinoense*) of 14:4:2:2:1. The blade exceeds the antennal tip by a distance as great as the length of the last segment. The various features of the labium, labrum, and epipharynx, seem to be identical in the two species.

The pupa of *P.* (*T.*) *digitifer* appears to differ from that of *P.* (*P.*) *illinoense* in the character of the caudo-lateral spur on the 8th segment in that *P. illinoense* has four main apical spines and several smaller subapical ones while *P. digitifer* has only three apical spines and two equally large subapical ones. *Polypedilum digitifer* has a smaller number of bristles in the swim fin (27 to 32 as compared to 40 to 45 described by Hauber) and distinct cephalic tubercles, which are small and nipple-like with a preapical bristle.

P. digitifer was another of the littoral forms found typically on a silty sand substratum (sand cenosis). Its seasonal distribution was atypical with the population maximum occurring in the spring and a minimum in the late fall. The maximum number of larvae dredged was 410 per square meter on May 7. This species apparently had several generations per year as evidenced by the collection of adults.

Adults were taken from February 9 to September 22.

Polypedilum (*Polypedilum*) *illinoense* (Malloch).—The immature stages were collected in sparse numbers on *Potamogeton.* The stages were as described by Hauber (1947) and Berg (1950).

Adults were collected from May 4 to August 9.

Tanytarsus (*Tribelos*) sp.—Adults of two species of the genus were collected, *Tanytarsus* (*Tribelos*) *fuscicornis* (Malloch) and *T.* (*Stictochironomus*) *palliatus* (Coq.). During the course of the investigation a larvae of *Tanytarsus* was collected which very much resembled, yet differed from, the described larvae of *T.* (*Tribelos*) *jucundus* var. *dimorphus.* At the time of the study, of the two species of adults collected, only the larva of *T. palliatus* had been described (Malloch, 1915; Johannsen, 1937). It was assumed that this undescribed larva was *T. fuscicornis* since the described *T. palliatus* larva differed considerably. However, Roback (1955) has since described the larva of *T. fuscicornis,* based on a reared female, which differs in several particulars from the Texoma species of *Tanytarsus.* From the scarcity of this

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[1] Berg (1950) described the larva of *P.* (*P.*) *illinoense* (Mall.) as new, apparently having overlooked Hauber's earlier paper.

previously undescribed larva it is concluded that the adult stage was not taken in the light traps so that a logical association cannot be made.

Mature larva: The length is 7 mm. The head is pale yellow except the occipital margin which is light brown and the labial and mandibular teeth which are black. The antennal socket is rounded and fairly prominent. Antennal ratio, 30:8:4:4:2; the blade reaches the middle of the 4th segment. The labrum has many curved bristles, 2 of which are pectinate. The epipharyngeal comb has 7 large teeth, most of which are trident due to the presence of basal denticles. The tips of the premandibles are strongly hooked. The mandibles and labial plate are as in *T. dimorphus* var. *jucundus;* and *T. nigricans* (Joh., 1937, Plate V, figs. 65 and 70). The paralabials are long, slightly curved and widely separated on the midline. The inner anterior tip of the paralabials are produced into a long filament-like structure which reaches the base of the 1st lateral tooth. The preanal papillae are very short, about as wide as long; each bears 8 bristles. There are 4 anal gills; the dorsal and ventral pair approximate in size.

The pupa was not associated.

Larvae occurred only in one collection from *Potamogeton.*

Tanytarsus (Tribelos) fuscicornis (Malloch).—Adults were collected from July 6 to September 1.

Tanytarsus (Stictochironomus) palliatus (Coq.).—The immature stages were not collected during the investigation. This was attributed to a very low population density and/or inadequate sampling of certain cenoses.

Adults were collected only on August 19 and 20.

Stenochironomus macateei (Malloch).—During this investigation, a larva was collected and keyed in Johannsen (1937) to *Stenochironomus taeniapennis,* the only described larva for this genus (Townes, 1945). On close inspection, the larva showed characteristics different from those described for *S. taeniapennis.* Since only one adult, *S. macateei* (Mall.), was collected at Texoma, this previously undescribed larva was associated with it.

Larva: The length is 3.5 to 4 mm. The head is brown and subcircular in outline. The antennae are six-segmented, the segments having a ratio of 13:5:5:2:3:2. The blade extends to the middle of the 6th segment. Other features are indistinguishable from *S. taeniapennis.*

The pupa was unassociated.

Adults were collected from July 12 to September 1.

Larvae occurred on silty or gravelly sand in the littoral zone down to a maximum depth of eight meters.

Xenochironomus festivus (Say).—This larva was very briefly described by Malloch (1915) as *Chironomus* sp. B from material dredged in the Illinois River. The following is given to supplement his description: Larva: The length is 20 mm. The color is reddish in life, fading to a yellowish-brown upon alcoholic preservation. The head capsule is yellow-brown. The tips of the mandibles and labium are dark brown to black. Antennal ratio, 63:18:5:7:3; the blade reaches the apex of the 3rd segment; the basal segment distinctly curved (Malloch, 1915, Plate XXX, fig. 6). The maxillary palp

as illustrated by Malloch (1915, Plate XXX, fig. 5); the basal joint arising from a low rounded tubercle. This tubercle is covered with numerous hairs which are as long as the basal joint of the palpus. The labrum and epipharyngeal area as figured by Malloch (1915, Plate XXIII, fig. 7). The epipharyngeal comb bears about 22 sharp teeth; the premandibles are distinctly toothed and bear a heavy brush. The labial plate as shown by Malloch (1915, Plate XXIX, fig. 5). The paralabial plates are very wide, coarsely striated, and separated by about a distance equal to the width of the trilobed central tooth.

Pupa: One pupal exuvia was recovered which, because of its size, may be associated with this species. The length is 22 mm. The cephalic tubercles are small, acute, and with a preapical bristle. The respiratory organs are numerous white filaments. The swim fin has in excess of 150 white bristles. The lateral margins of the 8th segment bears 3 large and 2 small filaments. The posterior-lateral angle bears a spur made up of about 30 coalesced spines, the spines distinct at the tips. Except for the large number of spines in the spur and the size, this description would fit several typical members of *Tendipes* (*Tendipes*).

The ecology of *X. festivus* was more unusual than that of any other tendipedid species encountered in Lake Texoma. This is the only large tendipedid found in the vicinity of the lake. Since its larval stages had not been described, the author sought a large larva to associate. For a greater part of the investigation, none was found. On March 17, 1951, while examining a shoal area exposed by low water, it was noticed that numerous keyhole-shaped burrows honeycombed a clay hardpan area. Each of these burrows was found to contain a large reddish larva which undulated its body in the characteristic movements of a plankton feeding, tubicolous tendipedid. Upon examination, these proved to be identical with *Chironomus* sp. B (of Malloch). Since *X. festivus* was the only large adult tendipedid found on the lake, this large larva is associated with it.

Malloch (1915) records his sp. B as having been dredged from the Illinois River and Townes (1945) says, "according to my experience, this species breeds only in large rivers." The presence of *X. festivus* in Texoma can be explained by its habitat location, i.e., wind swept clay hardpan shoals. These areas duplicate the conditions of a large river just as do the gravel areas for *Stenonema*, a typical swift stream mayfly.

Since the hardpan could not be dredged (with the Ekman used) seasonal distribution of the larvae cannot be given.

Adults were collected from July 6 to November 19.

Cryptochironomus.—Four species of this genus were collected as adults at Texoma: *C. blarina* Townes, *C. sorex* Townes, *C. fulvus* (Johannsen) and an apparently undescribed species. However, only one discernible larval type was collected. This type does not differ in any of the particulars described by Johannsen (1937) for *C. digitatus* (Mall.) and *C. fulvus* (Joh.). Since an association cannot be logically given this larval type is designated *C.* sp.

C. sp. was found to be a distinct littoral form occurring down to a depth of six meters. The substratum preference was silty sand and gravel with a few individuals occurring in gravelly sand. A seasonal distribution curve

plotted for this species showed a distinct bimodality with the two peaks occurring at December 18 and May 7. This bimodal curve is suggestive of a multiple species composition.

Adults of *C. fulvus* were collected from May 4 to September 1; *C. blarina*, from July 6 to September 1; *C. sorex*, May 4 to September 1; and *C. sp.*, July 6 to September 1.

Cryptochironomus, sens. lat. sp. b Joh.—A larva which agreed in all particulars with Johannsen's (1937) description was taken from the stomach of a blue sucker, *Cycleptus elongatus* (LeS.). This larva, while not actually collected from the lake floor, was found associated with several typical sand and gravel cenosis inhabitants in the fish's stomach. Its absence in dredging samples can be explained by its known habitat, i.e., under bark of submerged logs (Johannsen, 1937; Roback, 1953a).

Tendipes (Limnochironomus) neomodestus (Mall.).—The larval, pupal, and adult stages of this species that were collected agreed with the description given by Johannsen (1937) and Hauber and Morrissey (1945) for the larva and pupa, and Townes (1945) and Hauber and Morrissey (1945) for the adult. The larvae, which were restricted to the littoral, exhibited a definite substratum preference with the largest numbers occurring on silty sand. Although a preference was shown for this substratum, individuals were taken in other cenoses. The order in decreasing abundance of individuals collected was gravelly sand, *Potamogeton*, and gravel. The larvae had a regular seasonal distribution with a maximum number of 825 individuals per square meter being recorded on December 18.

Adults were collected from April 16 to September 23.

Tendipes (Limnochironomus) nervosus (Staeger).—The distribution of this species agreed with the preceding species in all particulars except that the maximum number of larvae was much smaller, 75 per square meter.

Adults were collected from February 2 to November 12.

Tendipes (Tendipes) decorus (Joh.).—In Texoma, this species showed the least depth preference of any studied. Specimens were collected from the water's edge to the maximum depth studied, twenty meters. The species showed a decided substratum preference, however, being restricted to mud and sandy silt bottoms. Although *Tendipes decorus* occurred in the littoral zone, it should be considered a profundal inhabitant since maximum numbers were found there. The seasonal distribution of *T. decorus* was very regular with a maximum number of 575 individuals per square meter recorded on December 3 and a minimum of less than 10 per square meter from July 19 to September 8.

Adults were collected from March 17 to November 19 with maximum emergence in early July.

Tendipes (Tendipes) plumosus (Linné).—Two specimens of the variety *T. (T.) plumosus* var. *ferrugineovittatus* (Zett.) were collected during the study. These were at Station I, Rock Creek bay, Washita arm. Since no other specimens have been dredged or adults taken in light traps, it probably

was a river form occurring in the lake only in the immediate vicinity of the inflowing Washita River. The two specimens were collected from a silty-mud bottom at seven meters depth.

Adults were not collected.

Glyptotendipes (*Phytotendipes*) *paripes* (Edw.).—This previously un-described larva is very similar to *G.* (*P.*) *lobiferus* (Say) as described by Johannsen (1937). It differs in the following particulars: The tips of the premandibles are heavily chitinized and blackened. Antennal ratio, 28:10:6:5:2; the blade extends almost to the tip of the 4th segment. The accessory tooth is short and broad but not notched. The labial bristle is in line with the last lateral tooth of the labial plate.

The pupa is also similar to that of *G.* (*P.*) *lobiferus*. It differs as follows: The length is 8 mm. The length of maces on tergites 2 to 6 in their respective orders are, 0.135, 0.15, 0.165, 0.21, and 0.375 mm.

The larvae of *G. paripes* occurred most frequently on *Potamogeton*, being one of the most typical forms in the cenosis. Specimens were also collected from sand and gravelly sand bottoms. It was restricted to the littoral.

Adults were collected from July 6 to November 2.

Harnischia (*Harnischia*).—The genus *Harnischia* was divided into the subgenera *Cladopelma* and *Harnischia* by Townes (1945). In his check list he listed ten species under *Cladopelma* and 27 under *Harnischia*. The im-mature stages of nearctic *Cladopelma* are unknown; two species of *Harnischia* have been described.

During this investigation adults of four species of *Harnischia* (*Harnischia*) were collected, *H.* (*H.*) *incidata* Townes, *H.* (*H.*) *carinata* Townes, *H.* (*H.*) *nigrovittata* (Mall.), and *H.* (*H.*) *monochromus* (Van der Wulp). None of these species have been described in the immature stages. Larval collections revealed two distinct forms herein described as *H.* (*H.*) *monochromus* and *H.* (*H.*) sp. The association of larva and adult of *H.* (*H.*) *monochromus* was based on these four reasons (1), *H.* (*H.*) *monochromus* was by far the most common adult; (2), the larva herein described as *H. monochromus* was the most common type of larva present in collections; (3), the herein described larva of *H. monochromus* was very similar to the described larva of *H.* (*H.*) *tenuicaudata* (Mall.); and (4), the adult of *H. monochromus* together with *H. tenuicaudata* and *H. potamogeti* Townes form a closely related group.

The larva described here as *Harnischia* sp. was clearly a member of the genus and subgenus and, undoubtedly, it is the immature stage of one of the remaining three species; however, no plausible association could be worked out.

The pupae of three of the four species were definitely associated by means of the visible male genitalia. These are *H. monochromus*, *H. incidata*, and *H. nigrovittata*.

Harnischia (*Harnischia*) *monochromus* (Van der Wulp).—Larva: The length is 3.5 to 4 mm. The head of the larva is yellow except for the labium which is dark brown and the mandibles which are yellowish-brown. The antennal ratio is 25:12:3:1:1. The blade extends to the middle of the 3rd

segment. The mandibles are rather strongly hooked, the mandibular teeth appearing as slight notches. A mandibular comb could not be detected in any of the specimens; however, the mandibles of this species are in an oblique plane, so this characteristic could have been overlooked. A compound brush is present, the branches being rather indistinct. A strong bristle is present on the convex side of the mandible, located at the basal fifth. The labial plate is similar to H. (H.) *tenuicaudata* differing in these respects (1), the central tooth is broadly trilobed; (2), the tips of the 1st lateral teeth reach only to the base of the indentation of the central tooth; and (3), the 4th and 6th lateral teeth are much shorter and smaller than the remaining teeth. The paralabials are slightly over 3 times as wide as long. Each preanal papilla has 8 bristles. At the base of each dorsal anal gill is a strong bristle.

Pupa (positive association, male genitalia visible) : The respiratory organs consist of tufts of about 20 white filaments each, arising from 6 main branches. The cephalic tubercles are small, slender, and acutely tipped; each bears an apical bristle. Segment 8 has 4 lateral bristles, with neither comb nor a spur. Lateral fringe of swim fin with about 30-35 bristles.

The depth distribution of H. *monochromus* was rather unusual. Specimens were collected from two to fifteen meter depth with a maximum number of 30 per square meter occurring at seven meters. From the distribution of the larvae and the structure of the larval mandibles a logical inference would be that these are predatory forms. A seasonal maximum of 80 larvae per square meter was recorded on May 7.

Adults were collected from July 26 to September 23.

Harnischia (*Harnischia*) sp.—The generic placement is based on the close similarity to H. (H.) *abortiva* (Mall.) as described by Johannsen (1937). This larva is probably the immature stage of one of the three species as discussed under *Harnischia* (*Harnischia*).

Larva: The length is 5 mm. The head is colorless except the labial plate and mandibular teeth which are black. The antennal segments have a ratio of 27:5:4:3:1. The 1st segment bears a blade and an accessory blade, both of which reach beyond the middle of the 3rd segment. The labial plate has 15 black teeth, the middle one almost twice as wide as the 1st lateral. The last lateral tooth of the plate is less than half the length of the adjacent tooth; other teeth of the plate gradually diminishing in size (as in Johannsen, 1937, Plate VII, fig. 100). The paralabial plate is slightly crenate on the anterior margin, about 2/5ths as long as wide. The striations are very coarse, each paralabial having about 10 striae. The anal gills are about 1/3 as long as the anal legs. The legs have strong yellowish brown claws. Each preanal papilla bears 7 long brown bristles.

This rarely collected larva was confined to the littoral zone and was found on gravel, gravelly sand, and *Potamogeton* substrata.

Pupa and adult were not associated.

Harnischia (*Harnischia*) *incidata* Townes.—The larva was unassociated. Pupa? (association based on visible male genitalia which apparently belong to this species). The length is 3 mm. The abdomen is green; the thorax, dark brown. The cephalic tubercles are long and slender, each with a short

preapical bristle. The respiratory organs are dichotomously branched, with over 20 ultimate branches to each organ. The 8th segment has 4 lateral bristles and a slender yellow spine on the posterior lateral border. Swim fin has about 40 bristles.

Adults were collected from May 7 to August 26.

Harnischia (Harnischia) nigrovittata (Malloch).—The larva was unassociated.

Pupa (association based on visible male genitalia): It differs from *H. (H.) incidata?* in that there are 2 spines on the posterio-lateral angle of the 8th segment, of which the anterior is smaller and straight; the posterior, rather long and sinuate. The swim fin has about 35 lateral bristles.

Adults were collected from May 7 to October 23.

Harnischia (Harnischia) carinata Townes—One adult of this species was collected on August 7. Larvae and pupae were not associated.

HEMIPTERA

Members of four families of aquatic bugs were collected: *Ranatra* sp. (immature) (Nepidae); *Belostoma testaceum* (Belostomatidae); *Rheumatobates hungerfordi* (Gerridae); and Corixidae. The first three species mentioned were found only on *Potamogeton* or on a silty sand shore with much detritus (over it in the case of *R. hungerfordi*). The corixids did not exhibit any substratum preference and were found in all littoral cenoses.

Hemiptera determinations were made by Dr. Leslie E. Ellis, Mississippi State College.

MEGALOPTERA
SIALIDAE

Sialis sp.—Only one specimen was collected. This was at Station V on a silty sand bottom in 2.3 meters of water.

Adults were not collected.

COLEOPTERA

Representatives of three families of aquatic beetles were collected: *Dineutus* sp. (Gyrinidae), *Haliplus* sp. (Haliplidae), *Berosus pugnax* (LeC.) and *Tropisternus* sp. (Hydrophilidae). All species typically occurred on silty sand bottoms with considerable detritus. Depth distribution was zero to three meters.

BENTHIC COMMUNITIES

LITTORAL BOTTOM (Chilile Systasis)

This group of communities or systasis has been defined as extending from the water's edge to a depth of six meters. This depth was selected as the limits for the systasis because the author felt that the criterion most frequently used, i.e., lakeward limits of rooted macrophytic aquatics, was too variable. The criterion used for this study was depth of wave action as demonstrated by the depth of major sand deposition (Sublette, 1955, fig. 5). While it is recognized that the depositional pattern will vary from situation to situation and from lake to lake, in the author's opinion it is more satis-

factory than the one of plant distribution. Even the limitations of percentage composition of the substratum would be arbitrary if it were not for the ultimate criterion, that is close agreement between substratum type and numbers and species of inhabitants (cf. Baker, 1918; Muttkowski, 1918; Adamstone, 1924; Rawson, 1930; Krecker and Lancaster, 1933; Shelford and Boesel, 1942).

Gravel Cenosis.—Because of the conditions of the substratum and the type of dredging equipment available, this community was sampled only qualitatively at irregular intervals.

Of all the many factors of the hydroclimate (Wasmund, 1934, *vide* Clements and Shelford, 1939) none is more operative in determining the extent and duration of the gravel cenosis than wave action and associated currents. The gravel shoal or bar is maintained by continual water movements which tend to remove the finer sediments to areas of lesser activity. It would appear that in the absence of more than moderate water movement, residual boulders, cobble, and pebbles of the original lake basin are soon covered with allochthonous and autochthonous sediments. This condition was observed at Lake Texoma since the gravel cenosis was found only facing open water of considerable extent. All of the small deep bays and inlets had the original boulder and gravel bottom covered to a variable extent with sand, silt, and detritus. The only apparent exception was where the shoreline tended to be precipitous.

The criterion of community difference (or similarity) is both a qualitative and quantitative difference of species composition as well as environmental difference. Qualitatively, this community differed in the presence of three species found in no other community within the lake. These were *Argia moesta?*, *Stenonema femoratum tripunctatum*, and *Spongilla lacustris*. Although a quantitative difference was not recorded due to inadequacy of sampling apparatus, frequency occurence (i.e., the number of collections in which a particular organism was collected) and observations indicated that certain species were abundantly represented most seasons of the year. These were *Physa halei*, *Caenis* sp., *Cyrnellus marginalis*, *Tendipes neomodestus*, *Cricotopus tricinctus*, and *Argia* spp. It seems that the majority of these latter species occurred in the gravel cenosis because the substratum offered a firm place for attachment, locomotion, feeding, or other vital processes. This was inferred because the other communities in which these animals also occurred, i.e., gravelly sand and *Potamogeton*, offered the same thing and little more.

Sand Cenosis.—Sampling indicated that this was the most extensive community of the littoral zone. The substratum varied from almost pure sand to sand with an admixture of silt, clay, and detritus. The homogeneous sand substratum occurred only on windswept shores, principally those facing south. Almost invariably, sampling from this area gave negative results. The only animal collected was *Oecetis inconspicua*, one of the sand-case inhabiting caddis flies.

The usual sand cenosis substratum consisted predominantly of sand with admixtures of silt, some clay, and autochthonous and allochthonous detritus.

A total of 59 species (or groups such as Heleidae, Corixidae, Hydracarina) was collected from the sand cenosis. Of these 59 species (or groups), 25 occurred in no other situation. These are: *Quadrula q. apiculata, Truncilla donaciformis, Leptodea laevissima, Anodonta corpulenta, A. imbecillis, Lymnaea modicella, Hydracarina, Brachycercus lacustris, Callibaetis montanus?, Siphlonurus* sp., *Panatala hymenea, Enallagma civile?, Erpetogomphus* sp., *Gomphus plagiatus, Chrysops* sp., *Stratiomyia* sp., *Tabanus* sp., Heleidae, *Calopsectra neoflavellus, C. bausei?, Stenochironomus macateei, Sialis* sp., *Dineutus* sp., *Haliplus* sp., *Tropisternus* sp. Six of the 59 species were typically found in the profundal and are recorded as present only because of a slight community overlap in the vicinity of the ecotone. This assemblage of animals, while showing variation in species composition from one site to another, maintained a recognizable identity. The same is true for the profundal assemblage, although showing less variability. Where the two communities come in contact there is some overlap for many species. This zone of transition from one community to the other is the sublittoral, of authors. The following from Eggleton (1934) demonstrates this. He says of Lancaster Lake:

". . . there were 6,585 animals per square meter of bottom at the 2 meter depth, which were recorded in the column for 'All others.' This category contained all animals present except Corethra, Chironomus, Protenthes, Tubificidae, and Sphaeriidae. It was a heterogeneous group and contained representatives from several phyla and from many orders of invertebrates. At 3 meters this group had decreased to a total of 308 individuals per square meter, and these were restricted to a very few orders, whereas at 4 meter depth none of them were present, and the entire benthic fauna had changed to the typical profundal benthic types."

In the author's opinion such a line of separation between distinct assemblages as described by Eggleston would constitute an ecotone between communities in the sense used in terrestrial or marine ecology (cf. Allee, et.al., 1949). Fig. 3 is presented to demonstrate the position of the ecotone between this and the mud cenosis. The depth distributions shown are those of a typical sand cenosis inhabitant, *Polypedilum digitifer*, and a typical mud inhabitant, *Pelopia stellata*.

This was the only littoral community in which both qualitative and quantitative sampling was done. Since it was the most typical littoral situation, remarks concerning this community are also generalizations about the littoral systasis. The sand community limits fluctuated considerably with changing water levels. The direct effect of this on most of the forms was not noticeable. Moon (1940) demonstrated that when hydrosols are denuded they acquire a fauna in a very short time. An observation at Texoma confirmed this. On June 9, 1951, a series of eight dredgings was made along a shoreline recently inundated by a rise in lake level. These samples showed an average of 139 organisms per square meter present in this recently flooded area indicating that there had been a recent invasion.

The indirect effects of water fluctuations on the fauna are more pronounced. An obvious effect on the fauna is the distribution of aquatic plants. Large fluctuation tends to eliminate many species of aquatic plants. A reduced flora is reflected in a reduced fauna while extensive growths of macrophytic aquatics tend to produce an abundant fauna (cf. Ball, 1948).
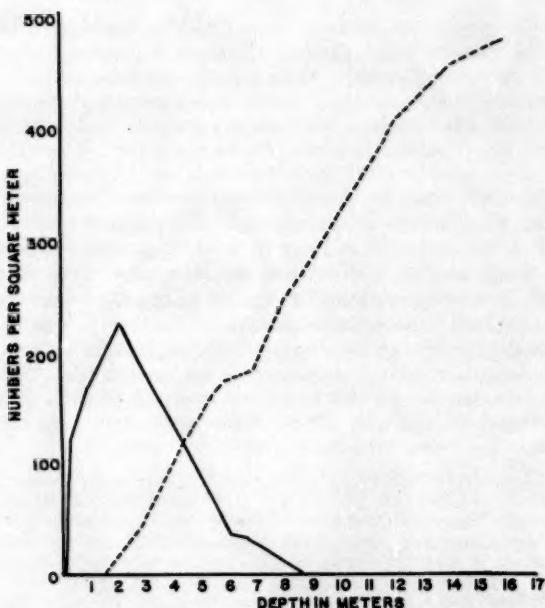
Fig. 3.—The depth distribution of two species of Tendipedidae (*Pelopia stellata*, dash line; *Polypedilum digitifer*, solid line) showing overlap of respective populations. This overlap is construed to be an ecotone. The distributions shown are smoothed curves of summer populations (June, July, 1949) as sampled at eight different localities in the lake.

Clay Consociation.—This community had a very limited distribution in the lake, being found only on windswept shores that were made up of residual clay hardpan. Away from windswept shores the absence of wave action soon caused the residual clay to become covered with sediments.

The Ekman dredge could not sample this substratum; hence, all results obtained by hand examinations were qualitative. Extensive examination revealed that only one species, *Xenochironomus festivus*, a large blood-red midge larva, normally inhabited this community. The distribution of this larva was unusual in that it showed distinct bunched distribution (cf. Miller, 1938; Ricker, 1952). This bunched distribution was clearly discernible on clay banks after the water level had receded. It appeared that the first (or early) instar larvae excavated their burrows shortly after leaving the site of oviposition. That the "colonies" were usually circular in outline would indicate that the larvae randomly wandered away from the site before the motivation for burrow construction terminated their wanderings. On large clay banks the "colony" pattern tended to disappear apparently due to overlapping individual broods. The distinct bunched "colony" was typical of small isolated patches of clay hardpan.

Potamogeton (*Emophyte*) *Cenosis.*—This discontinuous community which was found to be only locally prevalent was widely distributed in the lake.

It exhibited the least stability of any present in the lake, as a result of water draw down and winter die-back.

Samples taken in the *Potamogeton* beds disclosed the presence of 28 species of animals, of which only six were restricted to that particular habitat. These are: *Ancylus* sp., *Argia* sp., *Oecetis cinerascens*, *Orthotrichia* sp., *Hydrellia* sp., and *Tanytarsus* sp.

PROFUNDAL BOTTOM (*Mesopthmile Systasis*)

Mud Cenosis.—Of all substratum situations present in a lake, none is more adverse to most benthic species than the soft mud bottoms of deep water. In a temperate lake of the second order some of the adverse factors are: soft flocculent bottoms that will not support heavy bodied animals; low concentration or absence of dissolved oxygen; and high concentrations of carbon dioxide and other noxious substances. Since Texoma is a lake of the third order, most of these factors should not be operative. The physical and chemical data revealed that transitory thermal and chemical stratification occurred in many areas of the lake. However, the stratification pattern was not continuous but occurred only in areas with sufficient protection from the wind. Complete oxygen depletion did not occur although it was approached at Station IV. These transitory thermal stratifications and near stagnation in certain areas indicated that, while Lake Texoma was classified as a third order lake, it was very near the borderline between the second and third order. The distribution of the profundal fauna also supported the view. The normal sequence of distribution of bottom fauna for second order lakes was described by Eggleton (1931) while that of a third order was described by Adamstone (1924). The characteristic feature of the summer benthic fauna of a second order lake is a concentration zone (i.e., large numbers of individuals) in the upper profundal or lower littoral, while in a third order lake the fauna is more evenly distributed throughout the year. This has been explained for the
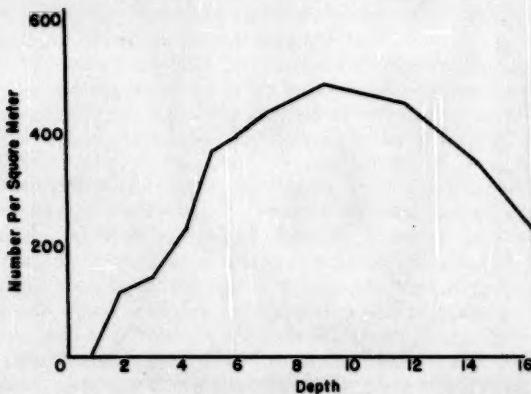
Fig. 4.—Depth distribution and relative abundance of *Chaoborus punctipennis* as shown by a smoothed curve of the summer population (June, July, 1949) of eight stations located throughout the lake.

second order lakes as a response to decreased oxygen content of the hypo-limnion; the animals migrating upward to escape the effects of decreased oxygen. Since oxygen was not exhausted, only lowered in the lower profundal region, it would be expected that the fauna would not show this distributional sequence as clearly as in lakes where a stratification sequence is well established. Two types of horizontal distribution were observed in the profundal area; one, exemplified by *Chaoborus punctipennis*, where the animals are apparently sensitive to lowered amounts of oxygen and the other, shown by *Pelopia stellata*, where the only distributional pattern was a response to depth and not to oxygen content of the water. These distributional patterns are given in figs. 3 and 4.

The species composition of the profundal fauna of Lake Texoma was very similar to that described for natural lakes of the second order (Welch, 1952). This deep water fauna was characterized by a relatively large number of individuals and by few species. Animals which have extensive distribution in the profundal area are: Oligochaeta, *Pelopia stellata, Pentaneura basalis?, Procladius bellus, Tendipes decorus, Harnischia* sp., *Hexagenia munda elegans, Chaoborus punctipennis, Coelotanypus* spp.

BOTTOM FAUNA PRODUCTION

Four stations were sampled at frequent intervals throughout the year. The figures expressing annual crop have been derived from 267 dredgings representing 75 samples taken at these stations, two samples having been taken in the littoral (sand cenosis) and two in the profundal systasis on each collecting date.
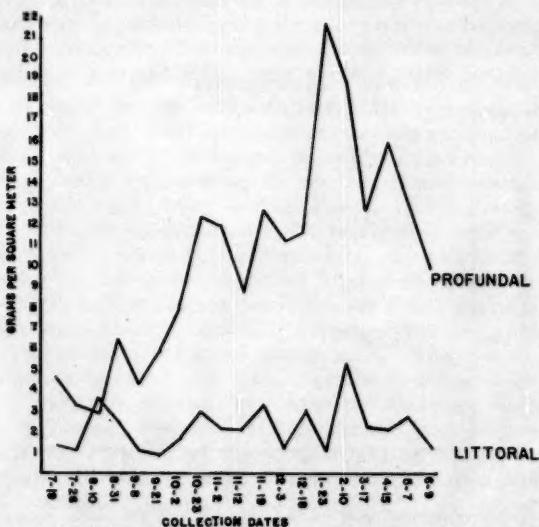
Fig. 5.—Annual standing crop from two communities, the sand cenosis (littoral) and mud cenosis (profundal).

Fig. 5 gives the annual standing crop of bottom fauna expressed in grams per square meter, and shows that Texoma has a winter maximum and summer minimum characteristic of many natural bodies of water. When total number of bottom organisms (fig. 1) is compared to weight (fig. 5) it will be seen that there is a close relationship.

Texoma had an annual mean standing crop of 21.75 kilograms of bottom fauna per hectare in the littoral community and 102.9 kilograms per hectare in the profundal. Townes (1938) considers a natural lake yielding 300 kilograms per hectare of bottom fauna to be "at least normally rich." When compared to such a standard Texoma appears to be rather poor. However, this standard may show a supposed, rather than a real, poorness. In Texoma three factors modify this standard: (1) Most of the submerged bottom is producing macroscopic benthic organisms because of a lack of stagnation, (2) the rate of turnover is much higher in southern waters, and (3) many of the benthic organisms are large enough to be readily available (*Hexagenia* spp., *Coelotanypus* spp., *Pentaneura* spp., *Tendipes* spp., and others). Townes (1938) says concerning this size-availability relationship:

"Chautauqua is a lake unusually rich in invertebrate fish food . . . with an average of 39 grams per square meter [390/kgm/ha] . . . in spite of its richness, Chautauqua is poor in certain features. Its profundal fauna contains less *Chironomus* [=*Tendipes*] *plumosus* than does that of many lakes. There are practically no burrowing mayflies, few polycentropid caddisflies and surprisingly few dragonflies in the lake."

His implication was that although Chautauqua supported a large benthic biomass, it did not contribute proportionally to the next consumer level, the fish population. The reverse may be true at Texoma, where a small benthic biomass is present contributing a much larger proportion to the next trophic level(s).

SUMMARY

The results of a fifteen months study on Lake Texoma, Oklahoma and Texas, are presented. Emphasis has been placed on the horizontal distribution and seasonal changes of the benthic invertebrates.

The waters circulate almost continuously throughout the year, with some tendency for stratification to occur, at least in areas that have some protection from the prevailing winds. This tendency is reflected to some extent in the composition and distribution of the bottom fauna, at least in the profundal area. In this region of the lake floor, the benthos is of a limited quality (indicative of lessened amounts of oxygen—only a few species are tolerant to lowered oxygen content) and compared to other cenoses of the lake, of relatively large quantity throughout the year (showing the absence of complete stagnation). In addition, this profundal community does not develop a concentration zone, again showing a lack of complete stagnation.

A total of eighty-seven species (or groups) of macroscopic benthic invertebrates was collected. Of this number, the insects predominate with seventy species. Brief autecological notes are presented for each species or group. To determine many insect species in the larval or nymphal stages, adults were collected by light traps and sweepings and associated. The immature stages of twelve species and one genus are described for the first time. Three additional species are associated from previous *incertae sedis* descriptions.

The benthic communities are classified according to a modification of Klugh's (1923) outline. These communities are named after the substratum composition for which criteria were modified from Roelofs (1944) and the Bureau of Soils Classification (*vide* Turnbull, 1944). It was found that the distribution of the bottom fauna followed closely the character of the substratum with each principal substratum type showing both qualitative and quantitative differences. The substratum type in turn was dependent upon the nature of the original lake basin as modified by certain environmental factors, notably depth and wave action.

Data are presented to demonstrate the presence of ecotones. Those between adjacent cenoses are rather poorly defined, but those between the littoral and profundal systases are well defined. This latter ecotone is considered to be the equivalent of the sublittoral zone, of authors.

The annual standing crop of bottom fauna from two cenoses is given. The minimum standing crop was found in the late summer and the maximum in late winter and early spring. It is suggested that although this production figure is low, the lake is probably more productive in the next trophic level (fish) due to certain of the modifying factors that would be expected from the amount of benthos produced.

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The Use of Non-Morphological Attributes
For the Recognition of Myxosporidian Species

Paul A. Meglitsch
Drake University, Des Moines, Iowa

The practicing taxonomist must discover dependable attributes and descriptive techniques which will permit his colleagues to identify accurately the species which he describes. It is inevitable that the nature of the species concept which he entertains will have much to do with his evaluation ot traits used in his species descriptions. In some groups the most careful morphological work still leaves much to be desired. This is the case with the Myxosporidia, for the small size and simplicity of the structure of the spore makes it extremely difficult to adequately describe species. Fortunately, a great deal of thought has been devoted to the development of more adequate concepts of the nature of the species group in the past few decades. This makes it possible, today, to consider the dependability of traits other than morphological ones for the description of species. The author (1954) has attempted to characterize the species group in such a manner that uniparental as well as biparental organisms are included. The following discussion is based upon the idea that the species group is an independent and distinctive biological region of gene spread, regardless of the mechanisms which may be involved in furthering this spread or in retarding it, and that it is therefore a unit in the evolutionary process. To permit this it is necessary that any gene may, in the dimension of time, come to replace its allelomorphic genes should they become adaptive. This means that the species is a group of organisms which does, or can, inhabit a common geographical (or, in parasitic forms) biological distribution area, within which the patterns of intra-group or extra-group competition and cooperation facilitate selection of satisfactory gene constellations. When some portion of the original species group acquires characteristics which permit it to exploit an environmental niche denied to the parental strain an incipient species has been produced. This incipient species may or may not become a distinct species. If the new strain withdraws from competition with the parental strain by becoming restricted to its new ecological niche or if it loses contact with the parental strain over a considerable portion of the original distribution area, it loses its potentiality of replacing the parental strain and must be thought of as a distinct entity. It may seem that the unity of the species, in uniparental organisms such as the Myxosporidia, is less definite than in the biparental species, since there is no integration of the population by interbreeding. In the long run, however, in both interbreeding and uniparental organisms the species is a group of organisms with a large number of common genes descended from common ancestors, which evolves as a group, rapidly or slowly depending upon the degree of harmony which marks the internal physiological interrelationships and the external ecological interrelationships which the species maintains.

Morphological attributes have long predominated in serving as criteria for the recognition of species. As we have learned to visualize the species

as a functional unit in the evolutionary process, however, we tend to find that morphological attributes alone do not suffice for species recognition. Accordingly other marks of species differentiation are sought. Ecological characters, e.g. the geographical distribution of organisms and the ecological niche into which they fit, are sought. Physiological traits are also utilized when discovered. Among parasitic organisms, like the Myxosporidia, ecological and physiological characteristics are often best reflected by studies of distribution and of host- and organ-specificity. Needless to say these data have been applied very differently by investigators in the past, and a good deal of difference of opinion still exists concerning their taxonomic value. It is intended here to discuss some of these points, with a view toward stimulating further discussion upon them and eventually establishing more uniformity in their interpretation.

THE INTERPRETATION OF HOST-SPECIFICITY

The fact that most Myxosporidia are known to occur in but one or two host species is not merely a reflection of the incompleteness of our data. Investigators have been recording observations of Myxosporidia for more than a century, and during this span thousands of fishes have been examined from all parts of the world. The body of accumulated evidence is very extensive, particularly as it relates to the more common fresh-water fishes and marine fishes from the littoral zone. It is possible, therefore, to state that in general the Myxosporidia exhibit a rather marked host-specificity.

The factors responsible for the phenomenon of host-specificity are, in a large measure, unknown. It may be assumed that ecological and physiological factors are both concerned. The extent to which the behavior patterns of potential hosts affect the possibilities of their being exposed to infection with Myxosporidia is as yet a virgin field for study. Some information exists, however, which strongly suggests that ecological factors relating to the distribution and behavior of potential hosts are less critical in producing host-specificity than are physiological factors. Bond (1937) found that when a number of species of fishes which were normally associated with *Fundulus* in Chesapeake Bay were exposed to parasites taken from *Fundulus heteroclitus*, only other species of *Fundulus* could be infected. In this one experiment, at least, it was demonstrable that physiological incompatabilities were of importance in preventing infection. Actually this is to be expected if one considers the more extensive data gathered by other parasitologists working with helminths.

Inasmuch as some species of Myxosporidia have been described from several host species the discovery of a parasite in a new host species cannot, in itself, be considered as evidence that it is a new species. Nevertheless, if the new form is found to be morphologically similar to some species known only from a host which is not closely related to the new host, cross infection experiments, if practicable, should be made. This has not been standard procedure in the past, and has resulted in a degree of uncertainty concerning the validity of some species identifications. It seems quite possible that the many different collections of such species as *Myxidium lieberkuhni*, taken from many different host fishes, may represent several distinctive species, all

exhibiting marked morphological similarities. Certainly when one is faced
with the problem of designating a name for a myxosporidian parasite which
is morphologically similar to a species described from some other host, not
closely related, a strong suspicion that the two are different should be held.
The taxonomist, in such a situation, cannot fail to be embarrassed without
conducting cross-infection experiments, for to designate the new strain as a
new species requires him to assume that the new strain will not and does not
infect the species of fish inhabited by the known strain, while to designate the
new strain as belonging to the known species requires that he assume that
cross-infection does occur. In the absence of data, it is difficult to justify
either assumption. Certainly a very careful study of the new strain for
evidences of distinguishing morphological traits is indicated, but if no such
differences can be found, it is almost as unlikely that two distinct strains
should be exactly the same in appearance as that the same species should
happen to be physiologically compatible with two host species which are not
closely related.

From time to time suggestions have been made concerning the development
of a trinomial system for parasitic forms, in which the last name be derived
from that of the host species. There is considerable merit in this suggestion,
in the sense that it will relieve us of the necessity of making either of the
assumptions mentioned above. It is my opinion that we should strongly
entertain the acceptance of this scheme, either as a standard procedure, or,
preferably, only in cases in which it is impossible to distinguish between two
parasites which live in different host species, and which have not been tested
by cross-infection experiments. There is much to be said for the use of
temporary trinomials. Their use would not disturb the historic binomial
system, for in all instances in which all of the necessary information is avail-
able, the ordinary binomial would be employed. When two or more morpho-
logically identical strains were found in different hosts, however, the trinomial
would be used automatically. As soon as cross-infection experiments were
completed, or when some distinguishing feature was discovered which indi-
cated that the two strains were not identical, appropriate binomials would be
designated for each strain. This system would avoid the very real difficulty
which would result from the routine use of trinomials based upon the host
species for all parasitic species. If they are routinely applied two morpho-
logically identical strains which inhabit different host species would always
have different names, whether or not they were actually part of the same
parasite population. With temporary trinomials the taxonomist is relieved
from the necessity of incorporating an assumption into his species designation,
as he must do without cross-infection experiments when only the binomial
system is used.

THE INTERPRETATION OF GEOGRAPHICAL RANGE

If we understand the species as a more or less homogeneous population
of organisms which evolves as a unit, it is evident its distribution in space
must be continuous. This spatial continuity, however, is not a simple conti-
nuity. Various kinds of factors may considerably complicate the situation,
making the analysis of the species population quite difficult. Many of these

kinds of factors have been discussed by the population geneticists and students of evolution working on various Metazoa or plants. Small local aggregations of a species population are developed which, for a time, are almost wholly isolated from similar aggregations not very far away. These local aggregations, however, in the absence of effective barriers, are not permanent and over a long period of time gene spread between organisms in various localities takes place. Where barriers occur divergence between different stocks is inevitable. It is evident that if divergence persists long enough incompatibility between the gametes of the various stocks will tend to arise. Long before there is any such incompatibility, however, physical traits which suffice to distinguish between the stocks often appear. While these and similar facts have been known and discussed for some time by taxonomists dealing with higher forms, students of the Protozoa, and especially those interested in parasitic forms, have tended to neglect this phase of their problems.

Every lake or pond containing Myxosporidia represents such a local aggregation, and specifically, an aggregation which is apparently isolated from other such aggregations by an effective barrier. Each of these aggregations will tend to evolve as a discrete unit. Nevertheless it is improbable that any taxonomist would wish to clutter the systematic structure by assigning specific or subspecific names to all of these geographical isolates. Certainly the host fishes are not distinguished by any such plethora of names. As a matter of fact the kind of distribution which occurs in the Myxosporidia of fresh-water lakes and ponds indicates that the parasites are transferred from one body of water to another. The writer, for instance, has studied green sunfish from a number of small lakes and ponds in Iowa and Illinois without once finding a pond free of *Chloromyxum trijugum*, assuming that a fair sample of specimens were studied. None of the strains of *Chloromyxum* found was significantly different than those first described by Kudo (1921). It is evident that, whatever the mechanisms of transfer may be, the spread of the parasite occurs more rapidly than morphological differentiation.

It is evident that considerable caution is needed if we are to consider distributional evidence in assigning specific names. Viable spores may be carried for considerable distances by water currents, and at the present we lack the information necessary to calculate the probable distances which a viable spore might be transported. We do not know how long a spore retains its viability; we have no measures of the specific gravity of spores, nor, in many instances, the direction and speed of water currents. Very little work on the longevity of spores has been reported. There is evidence that in some species spores undergo visible changes rather quickly after leaving the host, while in others no visible changes occur after relatively long periods of time. There is some possibility that these visible changes are associated with viability (see Auerbach, 1909), but specific data are nowhere available. Until it has been shown that spores cannot withstand drying and so be carried by air currents, or cannot withstand passage through the digestive tracts of piscivorous birds and mammals or scavenging insects, we cannot rule out the possibility of frequent overland transport. Among fresh-water fishes, moreover, the wholesale stocking of ponds by conservation departments and the use of immature fishes as bait further complicates the picture.

Nevertheless the implication is clear that a species population must have a more or less continuous distribution area if it is to remain a homogeneous population and evolve as a unit. It is no less applicable to uniparental species, in which gene spread takes place by simple replacement, than it is to biparental species, which interbreed. What attitude shall we take when two very similar samples of Myxosporidia are found in different host species separated by a great distance? Where the geographical range of the hosts do not overlap or approach one another at any point and there is no known bridge of additional hosts extending between the separated parasite populations, an intensive search for such a bridge, as well as an intensive search for distinguishing features between the two strains of Myxosporidia is certainly indicated. Should no distinguishing characters be found a strong case for recognition of the two strains as distinct species can be made. Isolated reproductively by the very nature of their life cycle and isolated in space as well, these two groups cannot conceivably be evolving as a single unit, and must in consequence be thought of as distinct entities. This point of view, of course, applies only to situations in which each strain occurs in a different host species.

Where morphological work fails to show distinguishing traits between two such strains, we might test them by cross-infection experiments, wherever possible. It is not unlikely that in most instances we would in this way locate physiological difference between the two isolated strains, for it seems improbable that two strains of parasites which are completely isolated geographically and are subjected to the different selective pressures occasioned by differences in host species and physical environments will have failed to develop morphological or physiological differences. In my opinion it would be necessary to prove that they are identical rather than to prove that they are different, and the initial step should be that of giving each strain species rank, unless a trinomial involving the host species were to be adopted. In this case the taxonomist would have an excellent system prepared in advance to take care of the problem. Most of us find that in searching the literature concerning ecological or physiological information it is more difficult to tease out the facts when one species has subsequently been divided than when two original species have been found to be identical. For this reason, if for no other, it would be preferable to give different specific names if no trinomial system is adopted.

If cross-infections are used to show that two morphologically identical forms which inhabit different host species which are geographically isolated from one another, we may expect, occasionally, to find that the two strains will inhabit either host. Here we have a clear case of incipient species, fated by their isolation to eventually become different, but not yet having achieved this difference. Until this differentiation has occurred, both strains should be classified in the same species. It is probable, however, that a permanent trinomial could be used to advantage in such cases. It would be necessary to distinguish this trinomial from the temporary trinomial which would be used to designate uncertainty about the identity of two forms living in different hosts. There are a number of simple techniques for achieving this. Temporary trinomials, for example, could be written without italics, while permanent trinomials could be italicised.

The discussion of these theoretical problems is not without practical significance to taxonomists today. An interesting case of morphological similarity between two populations which are apparently completely isolated geographically was reported by Fantham, Porter and Richardson (1939). A parasite identified as *Myxobolus ovoidalis* was obtained from Canadian fishes. This species was originally described by Fantham (1930) from another species of fish collected in South Africa. It was suggested that the two strains of *M. ovoidalis* must represent the remnants of an unusually widely distributed species, or that it is a remarkable case of convergence. In the absence of cross infection experiments, it would seem that identity of the two strains is controversial. If the system described above were to be adopted, the two strains would be designated by trinomials derived from the host species until future work showed either morphological differences or physiological differences, or demonstrated that the two strains were incapable of cross-infection, in which case the Canadian form would be given a new specific name of the ordinary binomial type, should differences have been found. Alternatively, if no differences are found and it appears that we are dealing with incipient species, new, permanent trinomials of subspecific rank would be assigned to each strain. However, until these differences had been sought for and critical information concerning them had been obtained, *Myxobolus ovoidalis* would remain a complex, consisting of two tentatively distinct types with corresponding temporary trinomial designations.

THE INTERPRETATION OF ORGAN-SPECIFICITY

Just as the selection of a host species implies the operation of physiological factors upon which compatabilities rest, so the choice of a host organ within the species must reflect physiological requirements or potentialities of the parasite. Myxosporidia differ greatly with respect to organ-specificity, some exhibiting it to a very marked degree, while other have the ability to tolerate the conditions found in many different organs. Despite the very great significance which organ-specificity might, in theory, have, experimental work directed toward its analysis is almost entirely lacking. Any discussion, therefore, must remain in theoretical terms to a large extent.

We may begin with the thesis, supported by all of the observational work so far, that all species are limited to a certain extent. Whether we think of their choice of a host species or their choice of a habitat within the host their limitations are more marked than their potentialities. It is evident that limiting factors are both numerous and powerful. In the choice of a host species, opportunity to infect is an important factor, no doubt. This factor will be taken into account if we consider geographical continuity or discontinuity in our interpretations of distributional data. In discussing opportunity to infect, it was pointed out that the little evidence we have points to the idea that the lack of opportunity to infect is, in general, less limiting than incompatabilities with potential hosts. In exactly the same manner we must visualize that incompatibilities between parasite and host organ are more limiting than lack of opportunity for the parasite to reach tissues that remain uninfected. Upon what do these incompatibilities depend?

There can be little doubt that the key to many of the limiting factors within the organism lies with Shelford's law of tolerance. For each physical factor or chemical material which is biologically active there will be upper and lower limits of tolerance which delineate the range within which the species may survive. In attempting the analysis of these factors, however, it is well to remember that the quantity of one substance which is limiting, either in the sense that there is too little or too much of it, is not a stable quantity, but may be dependent upon the quantity of some other substance which may replace it, or which may increase the need for it. A second principle, no less important, is the concept of interaction between host and parasite. The parasitized tissue may change, the infected host may develop new sources of resistance, the parasite itself may adapt to conditions within the host by modification of its metabolic activity.

Of the physical factors which might conceivably be of importance to the parasite, the light-temperature-humidity complex associated with seasonal climatic changes looms as the most important, certainly, in determining general distribution, but not necessarily in determining the choice of host organ. That the parasite is affected by seasonal changes is shown by the frequency with which differences in occurrence associated with seasons has been observed. It is not clear, however, whether this seasonal distribution stems directly from the effects of the climatic factors upon the parasite, or indirectly by effecting changes in the physiology of the host. Much remains to be done in this area. It is possible, but far from certain, that climatic differences are of importance in limiting some species to warm or cold waters. In the absence of definite information on the importance of physical factors as limiting agents in general distribution, it is doubly difficult to assess their importance in determining distribution within the host. Light, for example, might be of importance in restricting body surface parasites to their superficial position, or denying the body surface to parasites which prefer an internal site. There seems, however, to be no clear evidence that turbidity of the water from which host organisms are taken is associated with differences in the occurrence of superficial parasites. In the absence of data one can have no more than an opinion, but in the opinion of the writer the physical factors, in general, have little relationship to the site of infection, except perhaps, as they relate to the differences existing within the tissues themselves.

Chemical limiting factors, on the other hand, may be of great importance in determining organ-specificity as well as host-specificity. We might suppose that, in general, raw materials needed to sustain metabolism would be of considerable importance. These might be roughly classified as 1) respiratory requirements in the broadest possible sense, including oxygen levels, the existence of satisfactory hydrogen acceptors other than oxygen, and the degree to which carbon dioxide and other metabolites of a respiratory nature collect; 2) energy requirements, again in the broadest sense, including materials which are directly absorbable or digestible; 3) growth requirements, including the presence of specific substances which cannot be synthesized by the parasite and must be obtained from the host; and 4) others. So little is known of the nutrition of protozoa, especially among the lesser-known parasitic groups, that we may almost say that this whole field of analysis is virgin territory. We

may hazard a few guesses, of course, but they cannot be dignified by a more complimentary term. It is not impossible that the species which inhabit the body surface, either integument or branchiae, have somewhat higher oxygen requirements than internal parasites, but there is no evidence to support this idea. It is not impossible that the species which inhabit the gall bladder, and which, apparently may acquire tinted protoplasm from the absorption of substances from the bile, require these for their metabolism. Such an idea might help to explain the very sharp difference between the fauna of gall and urinary bladders, but, again, there is no evidence. It is certainly possible that differing proteinaceous compounds in different tissues are differently available to the enzyme systems of the parasites, but once again evidence is completely lacking. It is doubtful if any general field of investigation is so difficult to initiate for the Myxosporidia, or so promising once it can be undertaken. It may well be that no real progress can be made in this direction until we can develop adequate cultural techniques.

Chemical limitation may also result from an excess of certain compounds. Some parasites may shun certain tissues and seek others with lower concentrations of deleterious substances. Biliary parasites may avoid the excretory system because of an inability to tolerate urinary substances rather than because of their need for compounds present in the bile. Specific tissue proteins might restrict as well as facilitate the growth of a species. A search of the literature reveals no definite data on limiting factors of a chemical nature, although there are occasional statements of a purely hypothetical nature. Even the relatively well-known antibody mechanisms have not been sought, or, at least, results have not been published.

It may seem, at first, that in the face of all this ignorance one would be foolhardy indeed to attempt to use organ-specificity as a basis for taxonomic work. The fact remains that even though we cannot explain organ-specificity it has been observed and described frequently enough to permit considerable generalization. We may still be in the purely observational phase of scientific analysis in this field, but this does not invalidate the observational evidence which is now available.

Myxosporidia can be classed in two principal ecological groups: the histozoic group and the coelozoic group. Histozoic species are less stable in their choice of habitat within the host than coelozoic species, although there are many exceptions to this general rule. In some instances, e.g., a whole genus of histozoic forms will be restricted to one or a few tissue habitats (see Meglitsch, 1947a).

The histozoic species may be classed into two groups. One group of parasites occurs in the internal organs of the host, exclusive of the skeletal musculature. The other group is found in the skeletal musculature and either on the body surface or on the gills. The writer is not familiar with any species that cross the dividing line between these two groups, although many species inhabit two or more combinations of habitats within the distributional limitations of the group.

Among the internal parasites, the most stable forms insofar as organ specificity is concerned, are those found in the skeleton or the visceral mus-

culature. These parasites are almost always specific with respect to organ, and sometimes have a quite specific locus within the host organ. Species inhabiting other kinds of tissues vary from highly specific to quite variable distribution. A few species seem to be nearly indiscriminate in their choice of host organ, as long as it is within the peritoneal cavity. Inasmuch as some of the more widely distributed parasites of the body cavity are located in connective tissue or peritoneum, their failure to settle upon a favorite host organ may be less striking than appears on the surface. It is quite probable that the histological and physiological milieu of very different organs is quite similar insofar as the connective tissue or peritoneum is concerned.

Parasites of skeletal musculature and integument, on the other hand, are extremely capricious. Very similar species may exhibit quite different tolerances for host organs. *Kudoa clupeidae*, for example, is known only from skeletal muscle, although it has been reported from a number of host species, belonging to several different genera. *K. funduli*, on the other hand, has been found only in *Fundulus*, but it is regularly found in the fins as well as in the skeletal musculature (see Meglitsch, 1947a). Species like *K. funduli* which occur in the skeletal musculature and integument present several quite interesting problems. What obscure physiological similarities exist between skeletal musculature and fin integument in *Fundulus*? What are the differences between fin integument and general body integument which restricts the parasite to the fins? *K. funduli* is not an isolated case, for many of the histozoic parasites of the body surface show unusual combinations of habitats, or are found in unusually restricted habitats. *Henneguya exilis* is found in the integument covering the body surface but does not occur on head or fins. The same species is also found in the branchiae (Kudo, 1934). *Myxobolus congesticus* occurs only in the fins of its host, and, further, only in the unpaired fins. *Myxobolus mutabilis* is found only in the integument of the head and the paired fins (*op. cit*). *Myxobolus conspicuus* is found in the head integument only (*op. cit.*). These are startling and tantalizing observations, which tend to indicate the nature of some of our problems.

The fact that a group of parasites are found at the body surface and in the skeletal musculature, and that these species are not found in other internal organs, suggests that the respiratory environment may be limiting in these forms. It would appear that the striated muscle, with a high myoglobin content, may provide an environment quite different than the smooth muscle, with a significantly lower myoglobin level, and that in the presence of the abundant respiratory pigment an environment is produced which is, for respiration, perhaps, similar to that encountered on the gills or at the body surface. Study might well be directed toward this problem, as experimental procedures to test this hypothesis could easily be devised. On the other hand, even though there may be a respiratory limiting factor operating among these species, it is evident that this is by no means the whole story. The peculiar kinds of distributions on the body surface seem to indicate that there is a general similarity in branchial and integumental surfaces, but that there are specific differences between gills and body surface, and, further, between the head integument, the general body integument, the integument of the paired fins, and the integument of the unpaired fins. In some instances these specific

differences, whatever their nature, are not limiting, while in other cases they are limiting.

Where a species has been described from a single, or very few host organisms, it would certainly be unwise to attach much importance to the position which it assumes in the host. This is especially true of parasites inhabiting the body surface. However, when a species is known to have a definite locus within or upon the host, and when this is supported by the examination of a number of infected fishes, the position of the infection appears to be as stable and dependable as any other character, and might well be used for taxonomic purposes. Where a species which, from long experience, is known to occupy a very restricted habitat within the host, is found to be identical in appearance to a new strain occurring in a different host organ, it would seem advisable to delay a definite decision concerning their identity until cross infection experiments had been undertaken. This would be particularly indicated when one strain was located in the musculature or on the body surface, and the other strain was found in an internal organ. In such a case it would seem that the burden of proof would lie with the proponent of identity rather than the proponent of difference.

The coelozoic species are naturally divided into two groups: biliary parasites and urinary parasites. There is a significant difference in the chemical environment of these two systems and it is not surprising that the coelozoic forms are so perfectly split into two categories. Our evidence at the present seems strong enough to warrant our acceptance of a general rule that morphologically similar organisms, one of which is recovered from the biliary system while the other has been found in the urinary system, should be considered as separate species. If they were found to occur in the same host species in the same locality it would be wise to establish their identity or difference by conducting cross infection experiments.

The writer is aware of but one instance in the literature in which a species is reputed to occur in both urinary bladder and gall bladder. Fantham, Porter and Richardson (1940) describe a parasite taken from certain Canadian fishes as *Chloromyxum granulosum*. *C. granulosum* was first described by Davis (1917) and later by Meglitsch (1947) from material taken from two different host species, both from Beaufort, N.C., U.S.A. The North Carolina material contained *C. granulosum* only in the urinary bladder and mesonephric ducts. While it cannot be known with certainty that Davis examined the gall bladders of the fishes containing *C. granulosum*, the large number of species which he described from gall bladders strongly suggests that he did so. The writer's notes show that in every case in which *C. granulosum* was found in the urinary bladder the gall bladder had also been studied. The gall bladders of a number of other, uninfected hosts were also examined. Had *C. granulosum* taken in North Carolina occurred in the gall bladder as well as the urinary bladder, or had the Canadian collections showed *C. granulosum* in both gall and urinary bladders, the case for considering these two strains identical would be immeasurably stronger. The fact is that each of the strains is reported from one locality within the host, and under the circumstances it would seem much more desirable to consider the form described by Fantham, Porter and Richardson as a distinct species.

CONCLUSION

In cannot be denied that taxonomic work is likely to center primarily about the evaluation and interpretation of morphological attributes. Nevertheless, the complexities of the interrelationships which exist between the parasite and its biological and physical environment reveal physiological differences between strains of parasites in the form of data upon geographical distribution, host-specificity and organ-specificity. These physiological attributes are of no less value as clues to genetic differences in the strains of parasites than are morphological data. They constitute evidences of phenotypic diversity and deserve full consideration when we debate the propriety of designating a population as a species. Conclusions drawn from a study of geographical distribution, should, however, take into consideration the possible dissemination of spores by air currents, piscivorous or scavenging animals, and water currents, and should no doubt, be used especially when there is a failure of ordinary morphological methods to demonstrate differences and when there can be no question of the geographical isolation of the two populations. Similarly, conclusions which are based upon the choice of a host by a parasite, or the choice of organ with the host, should take into consideration the number of hosts which have been studied, the vagaries which the species under discussion tends to show in its choice of host and organ. With all of these kinds of data we should retain, as a general ruling principle, the idea that they are pertinent only as they help us to recognize two distinctive non-competing populations which are evolving as different units.

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Gambel Quail Disease and Parasite Investigations in Nevada[1]

Gordon W. Gullion
Nevada Fish and Game Commission, Elko

Diseases and parasites are often blamed for the rather severe population fluctuations that characterize the history of Gambel Quail (*Lophortyx gambelii*) behavior over a period of years. Although evidence obtained during the course of studies conducted on Nevada's deserts from 1950 to 1954 suggested that other factors are more important as population influences, a certain amount of information was obtained concerning diseases and parasites of this plumed quail.

TECHNIQUES

From 1950 to 1953, 61 Gambel Quail, from various parts of southern Nevada, were collected for necroscopic examination. Necrotomy of the digestive and respiratory tracts of 54 quail was made with the aid of a stereoscopic dissecting microscope. Another seven quail were examined grossly internally for indications of disease or parasite infestation.

Recovered helminth parasites were fixed (nematodes in hot, 10 percent ethyl alcohol, and cestodes in Bouin's fixative) and then stored in 10 percent ethyl alcohol until ready for further processing.

During this same period blood smears were taken from 125 live-trapped quail. Blood was obtained by puncturing the brachial vein at the elbow articulation, and the drop then smeared in the usual manner and air dried (Campbell and Lee, 1953).

All disease and parasite identifications were made by specialists.[2]

FINDINGS

Blood Parasites.—Of the 125 birds from which blood smears were taken, readings were obtained on 110, and 62 of these were found positive for quail malaria (*Haemoproteus lophortyx*). Blood smears were obtained from 60 wild-trapped quail taken at Carp, southern Lincoln County, for transplant to the Gold Butte area, Clark County, in February, 1951, and of these, only 3 were found to be free of *Haemoproteus* infection. Degree of infection ranged from light (class 'A', 1-10 per 10,000 red blood cells) to heavy (class 'D',

101-500 per 10,000 cells), with most of the birds falling into the medium classes ('B', 11-50, and 'C', 51-100 infected cells per 10,000 cells—38 of 57 infected birds). All five quail from which blood samples were taken in the Gold Butte area in early February, 1951, proved to be positive for this type of bird malaria. Infection of four birds was class 'A', with one quail showing a class 'C' infection.

In March, 1951, smears were made from 48 quail in the Rose and Eagle Valley areas in central Lincoln County. None of these birds showed indications of *Haemoproteus* infection.

In addition to the high incidence of malarial infection in the quail from the Carp area, three birds had microfilaria in their blood.

Intestinal Parasites.—Of 61 quail examined internally (by Dr. Records and project personnel) 26 were parasitized or diseased.

One quail was found with an inflammation of the ceca and rectum. Records believed (personal communication) that this condition was "rather suggestive of coccidiosis." Several species of coccidia are listed from the closely related California Quail (*Lophortyx californica*) by Levine (1953), but none is reported from Gambel Quail.

Cestodes were found in the intestinal tracts of three quail. These parasites were identified by Doran and McIntosh as "*Rhabdometra* sp., probably *R. odiosa.*" In one quail three specimens were found in the anterior small intestine whereas in the other birds these worms were located in the mid-portion, 12 tapeworms having been recovered from one quail. This is probably the same organism reported by Gorsuch (1934) from Gambel Quail in Arizona.

Twenty-one quail (including two of those infested with cestodes) were infested with nematodes. Records found cecal worms in five of seven birds submitted to him by W. Blair Low, former project leader. Dikmans (personal communication) reported the identification of these worms as "*Subulura* sp., probably *Subulura strongylina.*" Nematodes recovered from 16 Gambel Quail examined by project personnel were identified as *Aulonocephalus lindquisti* by Doran. Degree of infestation varied from a single roundworm, recorded from a cecal pouch, to a relatively massive infestation of 200 worms in one bird, scattered through both cecal diverticula (118), the small intestine (1), rectum (63), cloaca (6), and even in the intestinal mesentaries (12).

Although *Aulonocephalus lindquisti* has been reported from Scaled Quail (*Callipepla squamata*) by Campbell and Lee (1953) in New Mexico, it has not been reported from Gambel Quail. However, Gorsuch (1934) reports *Subulura strongylina* as · the "most common internal parasite" in Gambel Quail in Arizona. A recent letter from McIntosh states, "Until more is known about the old and inadequately described species *Subulura strongylina*, we prefer to use the name *Aulonocephalus lindquisti.*" Hence it seems probable that the nematodes recovered from Gambel Quail in Nevada are the same as those reported from the same species in Arizona by Gorsuch. These roundworms were most commonly located in the cecal pouches, however, they were also found scattered through the intestinal tract in five quail, in the intestinal mesentaries of two birds, free in the body cavity of two birds, and even in the lungs of one quail (by post-mortem migration?).

External Parasites.—Nevada's Gambel Quail appear to be quite free of infestation by mallophaga. Biting lice were found on only one of 69 collected birds examined, and were never noted on any of the almost 3,000 quail handled during the trapping and banding operations. Gorsuch (1934) found "biting bird lice . . . of two species . . . are common to Gambel quail at all seasons, occurring in 28 percent of all birds examined."

Louse flies (Hippoboscidae) occur in varying numbers over the Gambel Quail range in southern Nevada. No louse flies were found on 114 quail trapped in the Overton area, Clark County, in March, 1952, nor on 27 quail from near Searchlight, also in Clark County, trapped in February, 1953. In the Las Vegas area of Clark County, hippoboscid flies were recovered from 2.3 percent of the 259 quail handled in the winter of 1952, and 4.8 percent of the 21 birds trapped in the fall of 1952. No flies were found in this area on 156 quail trapped in the winter and spring of 1953.

In the Gold Butte area the incidence of hippoboscid infestation varied considerably from section to section. Of 254 quail handled in the Catclaw Spring section in October, 1952, 5.5 percent were found to carry louse flies. In the winter of 1953, the incidence among 354 quail trapped in this same section dropped to 3.1 percent, and among 461 quail trapped near Catclaw in September, 1954, the incidence was only 2.2 percent. In September, 1954, louse flies were found on 8.3 percent of 181 quail wild-trapped near Guzzler GB-11, 3 miles from Catclaw Spring. By contrast, the Cedar Basin section, 7 miles distant from the Catclaw area and 2,000 feet higher (at 4,200 feet elevation), proved to have a relatively high incidence of infestation. Of 72 quail handled in September, 1953, 23.6 percent were infested, and in early October, 1954, 21.1 percent of 180 quail carried louse flies.

Thorough examination was not made of each bird handled; in fact, this was seldom done, the records for infestation being based entirely upon notations of flies deserting their hosts, or scurrying among the feathers of a quail while it was being handled. Louse flies were mostly frequently noticed among the feathers of the rump and flanks. As nearly as could be determined all of the louse flies seen on Nevada's desert quail were of the species *Stilbometopa impressa.* No definite records of the occurrence of *Lynchia hirsuta,* the small louse fly known from California Quail, were obtained during this study. The large louse fly, *Stilbometeopa,* has been definitely shown to be a vector in the transmission of quail malaria from one bird to another (Herman and Rosen, 1949).

Ticks were commonly found on quail from the Gold Butte area, especially from the Pinon-Juniper and Oak Chaparral habitat types (Gullion, 1953) in the Cedar Basin area (where louse flies were also most frequently encountered!). One species of the fowl tick has been identified, *Argas persicus,* and one larval specimen representing the genus *Ixodes* was collected. The *Argas* ticks occurred as larvae and nymphs, and were most frequently found at the bases of the feathers in the neck and breast region. No effort was made to determine the degree of infestation, but it is known that some quail carried several dozens of these ticks. Gorsuch (1934) reports heavy infestations with the *Argas* ticks on Gambel Quail in Arizona during the winter months.

Miscellaneous Diseases.—Several miscellaneous ailments of quail were encountered during this study. One bird from Las Vegas Valley, collected in April, 1951, showed two necrotic areas under the lining of the gizzard, but no further pathology was determined.

Two quail trapped in the Searchlight area during March, 1952, died within six days after being placed in captivity. One was found to be very thin, and necropsy disclosed a hard lump at the anterior end of the gizzard. A fissure was found in the gizzard lining, with a small hemorrhagic area underneath. No evidence of helminth parasites could be found. The gizzard contained no food, only grit. The lungs of this bird were red and badly congested and the intestines were filled with a strange smelling gas, quite unlike the odor normally present in Gambel Quail intestines.

The second quail, when trapped, was noted to be curiously puffy and bloody around the back of its head and neck. This bird was sluggish and indecisive in its actions in the trap and it ate very lightly in captivity, dying three days after being captured. When examined, its gizzard still was full of green food obtained prior to its capture. Dr. Records examined the head and neck of this bird and diagnosed the condition as a "favus" infection. He states (personal communication), "On the basis of the appearance of the neck skin and the lids of the right eye plus a microscopic examination of scrapings and some of the feather bases, I believe it would be safe to class this as a case of favus."

Another quail was collected in June, 1952, 16 miles south of where the first specimen was obtained. This bird had a somewhat lighter "favus" infection than the earlier specimen. Subsequently during waterhole counts made in this general area during July and August, 1952, evidence of this affliction was noted on at least 18 of the 60 adult males observed. At one count site evidence of this condition was also noted on a few adult female quail.

Dr. Records suggested *Achorion gallinae*, the fungus generally found on domestic fowl, as the organism possibly involved here.

Two quail that died during water requirement experiments, were found to be heavily penetrated internally by an aspergillosis type of infection. Both birds were adult females, one having died at the end of a waterless period of 13 days, during which she gained weight for 8 days, then lost 69 grams (from 160 grams) in 4 days and died. The other bird was placed in a cage to relieve another female long subjected to waterless periods. This bird, put immediately onto a waterless diet, died within three days, losing 37 grams in that interval. Male quail occupying the same cages at the same time and undergoing the same tests were not affected and appeared to be in normal health when released about six months later.

In each the mold mycelia had penetrated all parts of the thoracic cavity and in one the mold was in all air sacs and even on the gizzard and intestines. Material preserved for identification was misplaced so the causative organism is unknown.

During trapping in the Las Vegas Valley in January, 1953, at least 13 quail with swollen or deformed toes and cankerous growths on feet and legs
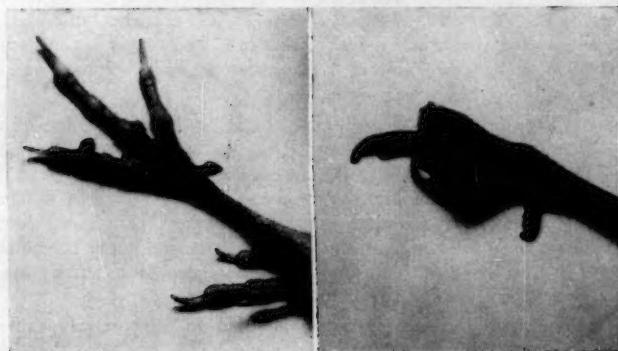
Fig. 1.—Possible bacterial lesions on feet and legs of Gambel Quail from near Las Vegas, Nevada. Note the loss of a claw from the toe of the bird on the right.

were observed (fig. 1). Two living, infected birds were submitted to Dr. Records for examination. His diagnosis was that of possible infection, and suggests the staphlococci as being "frequently responsible for multiple arthritis lesions" (personal communication).

Records further comments, "On the whole, I should be inclined to suspect this trouble was originally a bacterial infection, which in the case of these birds, had been overcome with complete healing except for the enlargement and deformity which persisted. Such an infection, however, is merely hypothetical, as we were unable to demonstrate any bacteria in one of the larger and apparently fresher lesions incised and examined for this purpose." Gorsuch (1934) suggests a similar ailment for one quail examined during his Arizona study.

DISCUSSION

It is evident that disease and parasites seem to be common in the life of Gambel Quail in southern Nevada. However, there were only two instances in which abnormal losses might be attributed to disease or parasites.

The continued decline of quail in the Carp area, where a 95 percent infection of quail malaria was found in mid-winter, 1951, might be attributed to this cause. However, it is suspected that the yearlong activities of transient, railroad section-hands against this narrowly confined, remote, canyon population may have had a more telling effect. Campbell and Lee (1953) state that the voluminous retake data on both *Haemoproteus*-positive and malaria-negative Gambel Quail gave no "reason to believe that avian malaria is a serious threat to Gambel quail *populations* in New Mexico. In fact, the bulk of this retake data points to the conclusion that malaria is definitely not such a threat, or at least was not during the period covered by this study."

Hungerford (1955) states, "Under normal conditions in good Gambel's

quail habitat, the blood parasite *Haemoproteus lophortyx* was not a mortality factor to be considered in southern Arizona quail management."

At least 3 of the 60 quail transplanted from Carp to the Gold Butte area survived for 2 or more years. Two known malaria-positive quail were retrapped. One having a light infection in February, 1951, was retaken in April, 1953, while the other, with a moderate class 'B' infection in 1951, was retrapped in late September, 1954. The third was bagged by a hunter on the last day of October, 1954, but its band had been lost (neck-tags remained) and positive identification was impossible.

The favus infection in the Searchlight area in 1952 noticeably reduced the vigor or affected birds and quite possibly could have made them markedly more vulnerable to predation. That such occurred was not demonstrated. It may be speculated that the moist spring of 1952 favored the dissemination and persistence of the fungal spores, and that the social antagonism and cock fights attendant to pair formation resulted in the wounds about the head and neck which permitted the establishment of the fungus in a warm, moist environment.

The role of helminths as decimating factors is probably unimportant as long as the birds maintain normal thrift through a sufficiency of food and water. Massive infestations might conceivably cause obstruction of the intestinal tract, with rupture the possible result. Gorsuch (1934) reports an enteritis in several quail in Arizona, suggesting possible secondary infection at the point where the scolex of the tapeworm, *Rhabdometra*, was imbedded.

Infestation by ectoparasites did not seem to affect the thrift of any of the birds examined, or at least, not noticeably so. The role of the louse flies as vectors for quail malaria has been reported by Campbell and Lee (1953).

It may be that the internal establishment of mold in the two experimental quail was the result of lowered vitality due to the nature of the experiments these birds were being subjected to. Why it didn't take a toll among other birds in the same and adjacent cages is not known.

SUMMARY

Sixty-two of the 110 Gambel Quail blood smears examined were found positive for *Haemoproteus lophortyx*. Microfilaria were found in the blood of three quail.

Of 61 quail examined internally, 26 were found infested with helminths. The nematode, *Aulonocephalus lindquisti*, occurred in 21 birds while a cestode tentatively identified as *Rhabdometra odiosa* was found in 3 quail.

External parasites occurred in varying numbers on Gambel Quail in southern Nevada, and included the big louse fly, *Stilbometopa impressa*, the fowl tick, *Argas persicus*, and a larval specimen of the tick genus *Ixodes*.

Six disease conditions of uncertain identification were encountered during four years of investigations. One of these was believed to be of bacterial nature (staphlococcus), one of protozoan nature (coccidian), two involved fungus infections (favus and aspergillosis) and two involved necrosis of the gizzard lining or its underlying tissues.

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Developmental Studies on Haemonchus contortus Rudolphi (1803)*

Joseph F. Berberian and John D. Mizelle
University of Notre Dame, Notre Dame, Indiana

Investigations on temperature and moisture requirements of *Haemonchus contortus* Rudolphi, have been meager (Veglia, 1915; Shorb, 1944) and in none was humidity carefully controlled. The present work was planned to determine temperature-humidity effects on the developing eggs and pre-parasitic larvae of this parasite, and to test the susceptibility of these life-history stages to several surface-active compounds.

MATERIALS AND METHODS

Ova (morula stage) were secured from live adult female *Haemonchus contortus* obtained from Armour and Company in Chicago, Illinois. Specimens were crushed on a glass plate and placed on cheese cloth through which the ova were washed into a 90 mm diameter petri dish, and then pipetted into 55 mm diameter petri dishes for experimentation.

The apparatus used for temperature-humidity studies was a Climatizer and its accompanying work chamber, both manufactured by the American Instrument Company, Silver Springs, Maryland (Seamster, 1950). The apparatus has a working range between 4.44-49°C, and is capable of maintaining relative humidities between 92-100% at 4.44°C, and 22-98% at 49°C. The apparatus maintained conditions of temperature which were accurate within ($\pm$) 0.14°C. Since humidities were obtained by temperature ranges between wet and dry bulb temperatures, they were controlled to a comparable degree. Recording thermometers were standardized by means of an Anschütz calibrated thermometer; relative humidity was checked against a hygroscopic humidigraph manufactured by the Bristol Company, Waterbury, Connecticut.

Wet and dry bulb thermometers situated within the work chamber were connected to an externally located, electrically operated thermograph which made 24-hour records of conditions inside the work chamber. This method of recording temperature permitted observation of conditions inside the work

chamber without opening the doors, and provided continuous daily records.

Two types of media were used: (1) tap water (high in carbonates), and (2) a feces-decoction filtrate prepared by boiling 10 grams of dried sheep feces in 100 ml of tap water from ten to fifteen minutes. The depth of medium did not exceed 3 mm since a depth greater than this prevents development of the eggs and larvae of *H. contortus* (Veglia, 1915). For temperature experiments, a minimum of twelve dishes of each type of medium was inoculated with approximately 200 ova each. Half of these were *covered* and the other half were exposed to the circulating air in the work chamber. Medium lost by evaporation during incubation was replaced to the 3 mm level in the petri dishes. Replenishing media were kept at the identical temperature of a given experiment in order to minimize temperature fluctuations. For each humidity experiment, a similar number of ova were smeared upon twenty fecal-smear slides (3 in. x 1½ in.). Control ova were kept at room temperature (21.1-23.9°C).

All observations were made directly from the petri dishes and smear slides with a binocular dissecting microscope equipped with 15x oculars and 1x and 8x objectives. Since the embryos and larvae did not all reach the same stage of development at the same time, those recorded on the data sheets represented the developmental stage of the majority of these present at a particular time except as otherwise noted.

The method of measuring development in the present work is Shelford's (1927) modification of temperature summing which was proposed by Reaumur about 200 years ago (Belehradek, 1935). It consists of conducting a series of experiments at a constant humidity and with varying temperatures. The reciprocal of the periods required for completion of development is plotted against the corresponding temperatures used (fig. 1), and the straight-line portion of the curve obtained is extended until it intersects the x-axis. Three or more trial temperatures (alphas) near the intersection of the curve extension and the x-axis are selected. Each of these values is subtracted from each of the temperatures used and the remainder is multiplied by the period involved. The correct alpha yields the most constant product (developmental total) for the several sets of figures.

This method utilizes "effective" temperatures only, and in addition provides for measuring development at temperatures on and beyond the straight-line portion of the curve.

By dividing the developmental total by the period required for development at a given temperature, one obtains the number of developmental units accomplished in one hour at this particular temperature. Shelford (1927) defined the developmental unit as, "the difference between the amount of development taking place in one hour at a given degree of mean medial temperature and the amount of development taking place in one hour at a temperature one degree higher . . ."

A velocity curve is constructed by plotting the number of developmental units accomplished in one hour, against the temperatures used. From a velocity
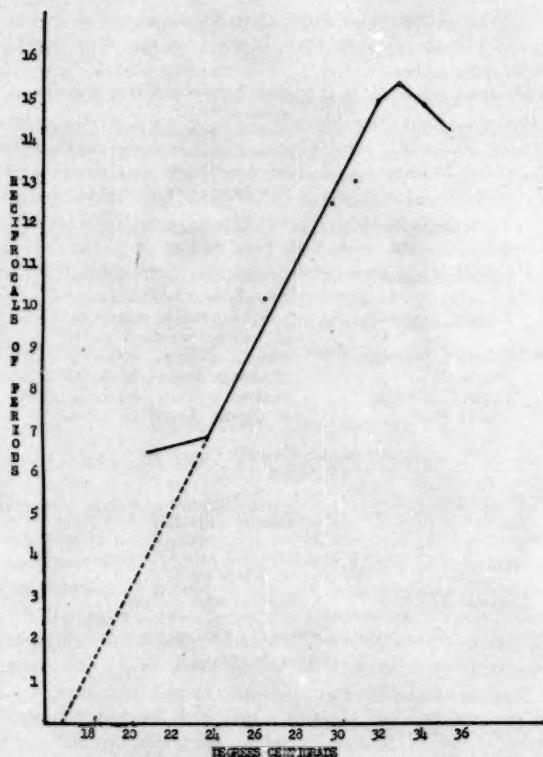
Fig. 1.—Reciprocals of periods required for development of infective larvae, plotted against the respective temperatures (in *covered* dishes of tap water). The broken line is an extension of the straight-line portion of the curve and is used in selection of the trial alphas.

curve one can predict the time required for completion of any particular stage of development at any temperature and humidity within the range at which development occurs.

A series of experiments were performed in which batches of *Haemonchus contortus* ova were exposed to each of sixteen constant temperatures ranging from 5.56° to 37.8°C with maximum intervals of 3.3°C and minimum intervals of 1.1°C as shown in table 1. These were incubated until appearance of the third-stage or infective larvae.

Surface-active agents were selected as the principal chemicals in this study because of their permeability-increasing capacity. These substances together with their respective manufacturers are as follows:

MONSANTO CHEMICAL COMPANY
St. Louis, Missouri

Chemical agent	*Chemical identity*
Areskap 100	mono-butyl-phenyl-phenol-sodium mono-sulfonate
Santomerse D	decyl-benzene-sodium-sulfonate
Santomerse 3	dodecyl-benzene-sodium sulfonate
Sterox CD	polyoxy-ethylene ester
Sterox SE	polyoxy-ethylene thioester

CARBIDE AND CARBON CHEMICALS COMPANY
New York, New York

"Tergitol" Penetrant 08	aqueous solution containing 38% of sodium octyl sulfate
"Tergitol" Penetrant 4	aqueous solution containing 25% of sodium tetradecyl sulfate
"Tergitol" Wetting Agent 7	aqueous solution containing 25% of sodium heptadecyl sulfate
"Tergitol" Wetting Agent P-28	aqueous solution containing 25% of sodium dioctyl phosphate

PROCTER AND GAMBLE COMPANY
Cincinnati, Ohio

| Orvus WA | active ingredient (sodium alkyl sulfate) |
| Product J | identity unknown |

E. I. DUPONT DE NEMOURS AND COMPANY
Wilmington, Delaware

| Duponol 80 | sodium octyl sulfate |

WYANDOTTE CHEMICALS CORPORATION
Wyandotte, Michigan

Ethylene dichloride	
Propylene dichloride	
C-7144-C	xylenesulfonic acid
C-1835-X-11	methyl benzenesulfonate
C-8765-CD	benzenesulfonylchloride
Solvent C100	90% or more aliphatic hydrocarbons principally propylene dichloride; 10% or less aromatic chlorinated hydrocarbons
Solvent C160	approx. 40% dichloroethers (2 pts. of 2,2^1-dichlorethyl ether: 1 pt. dichloroisopropyl ether), and 60% chlorinated hydrocarbons
Solvent R	50-60 2,2^1-dichloroisopropyl ether and 30-40% 2,2^1-dichloroethyl ether with small percentages of other compounds which give this solvent its dark color
Betachlor	approx. 60% 2,2^1-dichloroethyl ether and 40% 2,2^1-dichloroisopropyl ether

Other chemicals used were phenol, DDT, and copper sulfate. In one experiment phenol and copper sulfate were combined with Duponol 80 and tested against the ova.

Ova were removed from these experiments at intervals of 3 to 6 hours, and, after thorough washing in distilled water, were incubated at optimum developmental temperature (33.3°C) in order to determine viability.

In several experiments first- and second-stage larvae were tested in these compounds, but in all cases these were extremely susceptible to the chemical agents and were killed very rapidly in all concentrations above 0.1 percent. Further experiments with larvae of these stages were discontinued. Similar experiments were conducted with the more resistant infective (third-stage) larvae. Twenty-five to thirty of these were placed in individual petri dishes containing a given surface-active agent, phenol, copper sulfate or DDT. These experiments with larvae were conducted at optimum temperature (33.3°C) as determined in this study.

EFFECTS OF TEMPERATURE

Ova were exposed to a series of constant temperatures (5.56-37.8°C), at 100% relative humidity. Results varied somewhat for a given temperature. This variation generally was not as great between ova and larvae in the two types of media as it was with regard to the *covered* and *uncovered* dishes for a given medium (table 1). The incubation period at optimum temperature (33.3°C) was invariably shorter in the tap water medium. However, after the organisms in the feces-decoction filtrate (*covered* and *uncovered* containers) hatched, subsequent development was accelerated to the point that they attained the third-stage (infective) larva at the same time as those which developed in tap water contained in similar containers (table 2).

It is interesting to note that Veglia (1915) found water (tap, distilled) so unsatisfactory that he discarded it as a medium in his experiments. The present author is in agreement with regard to distilled water, but found tap water an excellent medium for development not only for embryos but also for larvae. The question immediately arises as to what the larvae fed upon and the only plausible answer is bacteria, since these were abundant in both media.

The difference in developmental rate in *covered* and *uncovered* containers was not very uniform. At some temperatures, *covered* and *uncovered* containers furnished conditions which allowed development in both types of media to proceed at the same rate. At other temperatures, development in *uncovered* dishes proceeded more rapidly than in *covered* dishes. At some temperatures, the *covered* dishes containing ova in feces-decoction filtrate were the only ones to lag in development while the *covered* containers of ova in water developed at the same rate as the ova in *uncovered* dishes containing both types of media (table 1).

VELOCITY OF DEVELOPMENT

The data obtained in this portion of the work were interpreted according to the procedures described on page 422. Data for ova developing in tap water contained in *covered* dishes provided a series of "constants" showing the least

Table 1.—Periods in hours required for development of ova and larvae of
Haemonchus contortus under different conditions

Time in hours and stage of development

Temper-ature °C.	Feces-decoction filtrate		Tap Water	
	Covered	Uncovered	Covered	Uncovered
37.8	120 (m)*	120 (m)*	120 (m)*	120 (m)*
36.7	132 (L1)	120 (L1)	132 (10%L3)	132 (L1)
35.6	80 (L3)	70 (L3)	70 (L3)	70 (L3)
34.4	75 (L3)	67 (L3)	67 (L3)	65.5(L3)
33.3	65 (L3)	60 (L3)	65 (L3)	60 (L3)
32.2	67 (L3)	61 (L3)	68 (L3)	64 (L3)
31.1	79 (L3)	77 (L3)	77 (L3)	77 (L3)
30.0	94 (L3)	80 (L3)	80 (L3)	80 (L3)
26.7	108 (L3)	90 (L3)	90 (L3)	90 (L3)
23.9	148 (L3)	148 (L3)	148 (L3)	148 (L3)
21.1	156 (L3)	156 (L3)	156 (L3)	156 (L3)
17.8	201.5(L3)	201.5(L3)	201.5(L1/L2)	201.5(L1/L2)
14.4	251 (1%L3)	251 (1%L3)	251 (L1)	251 (L1)
12.2	374 (1%L3)	374 (L2)	369 (L1)	369 (L1)
8.89	227 (5%L1)	275 (5%me)	252 (5%L1)	179 (5%me)
5.56	120 (m)*	120 (m)*	120 (m)*	120 (m)*

Symbols: L1—first-stage larva (= hatching); L2—second-stage larva; L3—third-stage larva; m—morula; im—incurved morula; v—vermiform; me—motile embryo.

deviation. The alpha in this case was 17.5°C, and the deviation did not exceed 28 units. Therefore, 1019 (± 28) was arbitrarily selected as the developmental total. This number represents the developmental units required for completion of development from the morula, as contained in freshly defecated feces, to the third-stage or infective larva of *Haemonchus contortus*—the whole process having proceeded in *covered* containers of tap water.

A velocity curve for development of *H. contortus* in *covered* dishes containing ova in tap water was then constructed by plotting the developmental units occurring in one hour on the y-axis and the temperatures on the x-axis (fig. 2).

The alpha chosen for developing ova in *uncovered* dishes of tap water was 21.5°C, and the corresponding developmental total was 706 (± 33). A velocity curve for development of *H. contortus* in *uncovered* dishes containing ova in water is shown in fig. 2.

Ova developing in *covered* dishes containing a feces-decoction filtrate yielded an alpha of 17.0°C, and a developmental total of 1081 (± 102). A velocity curve for *H. contortus* in *covered* dishes containing ova in feces-decoction filtrate is shown in fig. 3.

The alpha chosen for development of *H. contortus* ova in *uncovered* dishes containing a feces-decoction filtrate was 16.0°C, and the developmental

* No development beyond this stage; ova dead.
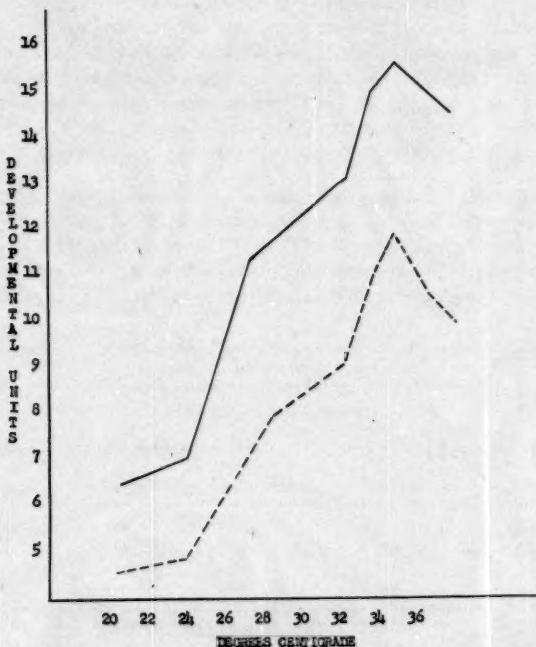
Fig. 2.—Velocity curve of development of *Haemonchus con-tortus* from ova (morula) to third-stage larvae in tap water. Solid line indicates development in covered dishes; broken line, in uncovered dishes. The difference in the height of the two curves is attributable to different developmental totals.

total was arbitrarily selected as 1074 (± 103). A velocity curve for developing ova of *H. contortus* in uncovered dishes containing a feces-decoction filtrate is shown in fig. 3.

The velocity curves provide a convenient reference for prediction of the time required to complete various stages of development in the life cycle under given conditions in each type of medium used.

DEVELOPMENT AT OPTIMUM TEMPERATURE

Optimum temperature as used in this study is defined as that temperature at which eggs (morula stage) of *Haemonchus contortus* develop to produce the infective or third-stage larvae in the shortest period of time. Optimum developmental conditions previously reported for this species may be interpreted in terms of optimum temperature since the authors (Veglia, 1915; Shorb, 1944) worked with saturated material. Veglia (1915) determined no definite optimum temperature but rather a range of temperatures which he
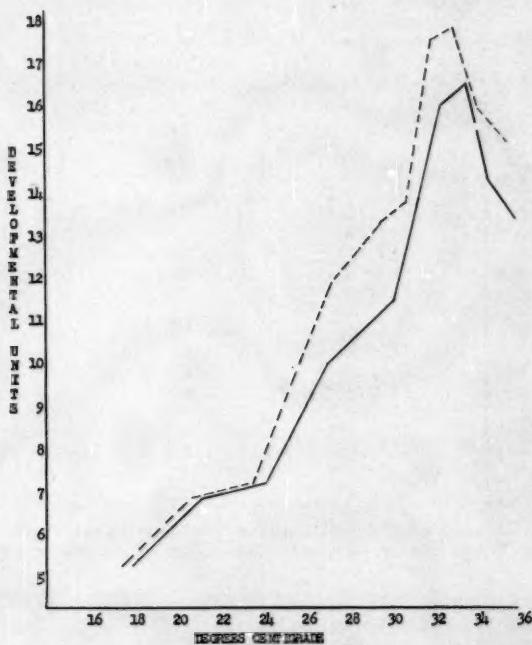
Fig. 3.—Velocity curve of development for *Haemonchus con-tortus* from ova (morula) to third-stage larvae in a feces-decoction filtrate. Solid line indicates development in covered dishes; broken line, in uncovered dishes.

cited as 20-35°C. He reported that ova from freshly passed feces incubated at 26-35°C developed infective or third-stage larvae in 3-5 days. Veglia's experiments apparently were not critically controlled since he stated, "From these notes it can be concluded that larvae of *Haemonchus contortus* can grow without showing any marked variations between temperatures of 22-35°C." It is not clear from his presentation whether or not he consistently used a constant-temperature apparatus as indicated by the tremendous temperature range he recorded for optimum development.

Shorb (1944) who consistently used a constant temperature oven in his studies also observed an optimum temperature range (21.1-26.7°C), with the moisture content being that of fresh fecal pellets, rather than a definite optimum temperature for development of eggs and larvae of *H. contortus*.

Utilizing temperature-humidity apparatus, the present authors observed 33.3°C at 100% relative humidity to be optimum temperature for the development of *H. contortus* in liquid media (tap water; feces-decoction filtrate). At this temperature infective larvae were produced in 60 hours in *uncovered*

dishes in both types of media (table 2). The same stage was reached five hours later (65 hrs.) in *covered* containers in both types of media (table 2).

Since ova used in the present work were initially at the same stage as those when passed in feces, it is concluded that conditions were not controlled with great accuracy in previous investigations.

Development at Temperatures Above Optimum

Infective larvae.—Inhibition of development and lethal effects of temperatures above optimum on *Haemonchus contortus* ova and larvae were reported by Veglia (1915) and Shorb (1944). The former author observed temperatures above 35°C to be unfavorable for development of *H. contortus* ova to the third-stage or infective larva. He found that only a "few" infective larvae

TABLE 2.—Development of ova and larvae of *Haemonchus contortus*
at optimum temperature (33.3°C)

| Period in Hours | Stage of Development | | | |
| | Feces-decoction filtrate | | Tap water | |
	Covered	Uncovered	Covered	Uncovered
1	m	m	m	m
2	m	m	m	m
3	m	m	m	m
4	m	m	m	m
5	m/im	m/im	m/im	m/im
6	im/v	im/v	im/v	im/v
7	v/me	v/me	v/me	v/me
8	v/me	v/me	v/me	v/me
9	me	me	me	me
10	me	me	me	me
11	me	me	me	me
12	me	me	me/L1	me/L1
13	me	me	L1	L1
14	me	me/L1	L1	L1
15	me	L1	L1	L1
17	L1	L1	L1	L1
22	L1	L2	L1/L2	L2
24	L1	L2	L1/L2	L2
36	L2	L2	L2	L2
39	L2	L2	L2	L2
60	L2	L3	L2	L3
65	L3	L3	L3	L3

Symbols as in table 1.

developed at 37°C; at 40°C eggs failed to develop; at 42°C the eggs were definitely killed, since they were checked for viability by subsequent exposure to 35°C. Shorb (1944) exposed freshly passed *H. contortus* eggs in fecal samples for variable periods, to constant temperatures ranging from 36.7-60°C and then removed them to room temperature for periods sufficient to allow surviving embryos to hatch and develop to the infective stage. After an exposure of "cultures" for one day at 36.7°C he recovered only 7,875 infective

larvae; after a two-day exposure at this temperature, only 8,400; whereas the controls yielded 14,310. No infective larvae were recovered from a "culture" exposed for 2.5 hours at 60°C before being removed to room temperature.

In the present work, ova incubated in *covered* dishes at 34.4°C developed third-stage larvae in 67 and 75 hours, respectively, in tap water and feces-decoction filtrate. At the same temperature, ova in *uncovered* dishes containing tap water and a feces-decoction filtrate, third-stage larvae developed in 65.5 and 67 hours, respectively (table 1).

At 35.6°C, ova incubated in *covered* dishes containing tap water and a feces-decoction filtrate, developed third-stage larvae in 70 and 80 hours, respectively. At the same temperature, ova in *uncovered* dishes containing tap water and a feces-decoction filtrate, third-stage larvae developed in 70 hours in each medium (table 1).

At 36.7°C, development proceeded to the first-stage larvae in both types of media in *covered* and *uncovered* dishes. In *covered* containers of tap water, second- and third-stage larvae appeared in small numbers (10%) in 132 hours (table 1).

The highest temperature used in the present work was 37.8°C at which development failed to occur and disintegration of the morulae was apparent after 120 hours exposure in *covered* and *uncovered* containers in both types of media.

The maximum temperature at which 100% of the ova and larvae of *H. contortus* were found to proceed to the infective stage was 35.6°C.

Eggs, first- and second-stage larvae.—Incubation periods for the ova and the periods required for development of the second-stage larvae of *H. contortus* at temperatures above optimum varied directly as the temperature.

At 34.4°C ova hatched in 12.5 hours in *covered* containers of tap water and 25 hours in feces-decoction filtrate. For the aqueous medium this was only one-half hour later than the period required for incubation at optimum temperature, whereas there was an 8-hour delay in the case of the feces-decoction medium. In *uncovered* dishes, hatching occurred in tap water and feces-decoction filtrate in 12.5 (12 hrs at optimum temp.), and 14.5 hours (14 hrs. at op. temp.) respectively. At this temperature, second-stage larvae were present in 36 hours in both media in *covered* and *uncovered* dishes. At optimum temperature, these larvae were produced in 22 hours (14 hrs. sooner) in *uncovered* dishes of tap water and feces-decoction filtrate, and in *covered* dishes in 22 and 36 hours, respectively, in the two media (table 3).

At 35.6°C hatching occurred in *covered* containers of tap water in 16 hours (12 hrs. at op. temp.), and in 25 hours in the feces-decoction filtrate (17 hrs. at op. temp.). In *uncovered* dishes, ova hatched in 14.5 hours in tap water (12 hrs. at op. temp.), and in 25 hours in feces-decoction filtrate (14 hrs. at op. temp.). Second-stage larvae appeared in 37.5 hours in both media in *covered* containers, whereas these appeared in 22 and 36 hours, respectively in covered containers of tap water and feces-decoction filtrate at optimum temperature. At 35.6°C these larvae developed in 23.5 hours in *uncovered* dishes of tap water (22 hrs. at op. temp.), and 37 hours in feces-decoction filtrate (22 hrs. at op. temp.) (table 3).

Ova incubated at 36.7°C hatched in *covered* and *uncovered* dishes in 15 hours in tap water (12 hrs. at op. temp.), and in 37 hours in feces-decoction filtrate (14-17 hrs. at op. temp.). Second-stage larvae appeared in *covered* dishes in tap water and feces-decoction filtrate in 43 and 60 hours, respectively at 36.7°C (22 and 36 hrs., respectively, at op. temp.). In *uncovered* containers these larvae were produced in 37 hours in tap water (22 hrs. at op. temp.), whereas none was produced in feces-decoction filtrate (table 3).

Embryogeny and the appearance of second-stage larvae were progressively retarded as the temperature was raised above the optimum. This retardation was more pronounced in the feces-decoction filtrate medium than in tap water, except for the production of second-stage larvae at 34.4-35.6°C (table 3). Since the feces-decoction filtrate afforded a good medium for putrefying bacteria and fungi it is suggested that this retardation may be due (in part) to toxic effects of the incompletely oxidized products of the putrefactive process (Michell, 1950). For respective media, the developmental periods were as long or longer for ova and larvae in *covered* than in *uncovered* dishes (table 3). Although the oxygen requirements of *H. contortus* ova and larvae have been reported to be very low (Veglia, 1915), it is possible that the greater retardation in *covered* containers was due to the combined effects of toxic compounds and a lack of oxygen.

TABLE 3.—Periods required for hatching, and development of second-stage larvae in different media at optimum and above-optimum temperatures

Temperature °C	Hours required for eggs to hatch			
	Feces-decoction filtrate		Tap water	
	Covered	Uncovered	Covered	Uncovered
33.3	17	14	12	12
34.4	25	14.5	12.5	12.5
35.6	25	25	16	14.5
36.7	37	37	15	15
	Hours required for development of second-stage larvae			
33.3	36	22	22	22
34.4	36	36	36	36
35.6	37.5	37	37.5	23.5
36.7	60	—	43	37

Development at Temperatures Below Optimum

Veglia (1915) and Shorb (1944) observed the effects of temperatures below the optimum on the ova and larvae of *Haemonchus contortus*, but made no permanent records of temperatures to which they were exposed. The former author utilized a "cold" (below 20°C) store-room in his investigations. He observed that infected sheep feces after four days at 15-18°C yielded "very few" infective larvae. At 8°C, he found "very few" second-stage larvae after 18-21 days and these developed no further when the temperature was raised to 35°C, the control temperature in his experiments. This

author reported no development at 4°C after incubation for 40 days. These ova were found non-viable when placed at 35°C. Shorb (1944) exposed *H. contortus* ova to temperatures ranging from -12.2°C to 12.8°C. He observed no development of infective larvae, and death resulted if the exposure was "sufficiently" long.

Dinaburg (1944) reported that under the influence of natural weather conditions, eggs of *H. contortus* did not survive exposure to temperatures below 21.1°C for more than 6 to 13 days.

In the present investigation eleven temperatures below the optimum (33.3°C) were used (table 1). The periods required for development of ova and larvae to the third-stage were progressively longer as the temperature was lowered.

At 32.2°C, third-stage larvae were produced in *covered* containers of tap water and feces-decoction filtrate in 68 and 67 hours,* respectively. In *uncovered* containers third-stage larvae appeared in 64 and 61 hours, respectively, in tap water and feces-decoction filtrate. Development at this temperature is the only instance in which third-stage or infective larvae appeared sooner in feces-decoction filtrate than in tap water (table 1).

At 31.1°C third-stage larvae appeared in *covered* dishes of tap water in 77 hours and in 79 hours in the feces-decoction filtrate. In *uncovered* dishes the third-stage larvae developed in 77 hours in both media (table 1).

At 30.0°C third-stage larvae were present in *covered* dishes of tap water and feces-decoction filtrate in 80 and 94 hours, respectively. In *uncovered* dishes third-stage larvae appeared in 80 hours in both media (table 1).

At 26.7°C third-stage larvae were produced in *covered* containers in 90 and 108 hours, respectively, in tap water and feces-decoction filtrate. In *uncovered* containers the same stage was reached in 90 hours in both media (table 1).

At 23.9°C third-stage larvae appeared in 148 hours in *covered* and *uncovered* dishes in both types of media (table 1).

At 21.1°C third-stage larvae were produced in 156 hours in *covered* and *uncovered* dishes in both media (table 1). Temperatures of 21.1°C and 23.8°C provided the only instances in which third-stage larvae appeared in the same time in *covered* and *uncovered* dishes in both media (table 1).

The minimum temperature at which 100% development proceeded to the third-stage larva in tap water in both *covered* and *uncovered* dishes was 21.1°C, whereas the minimum temperature for attainment of the same stage in the feces-decoction filtrate in *covered* and *uncovered* dishes was 17.8°C. At the latter temperature in *covered* and *uncovered* dishes of tap water, development proceeded to the second-stage larvae in 201.5 hours but no further.

At 14.4°C third-stage larvae were produced in only the feces-decoction filtrate in both *covered* and *uncovered* dishes in 251 hours in very small numbers (1%). In tap water, development proceeded only to the first-stage larvae in both *covered* and *uncovered* dishes in 251 hours (table 1).

At 12.2°C a few (1%) third-stage larvae were present in the *covered* dishes containing the feces-decoction filtrate in 374 hours. Larvae in all other

* See table 2 for periods required for development to these stages at optimum temperature (33.3°C).

preparations failed to reach the third-stage at this temperature (table 1).

At 8.89°C approximately 5% of the ova hatched in *covered* dishes in 252 hours in tap water and 227 hours in feces-decoction filtrate (table 1). Ova in *uncovered* dishes at the latter temperature failed to develop beyond the motile-embryo stage after 325.5 hours in each medium.

At 5.56°C ova in *covered* and *uncovered* dishes of both types of media failed to develop, and began disintegrating in 120 hours.

In experiments conducted at three temperatures below optimum (31.1°C, 30.0°C and 26.7°C) third-stage larvae appeared in the same time for a given temperature in all "cultures" except those in *covered* dishes containing feces-decoction filtrate. Production of third-stage larvae was retarded in the latter medium (table 1).

A series of experiments was devised to determine the retardation effect of 4°C on the development of *H. contortus* ova and larvae. In these experiments, ova in *covered* containers of feces-decoction filtrate were refrigerated at 4°C for periods of 11, 34, 59 and 82 hours and then removed to optimum temperature (33.3°C). *H. contortus* ova refrigerated for 11 hours before incubation, developed third-stage larvae in 72.5 hours (65 hrs. at op. temp.) while those refrigerated for 34 hours attained the third-stage at 97 hours of incubation. After 59 hours refrigeration at 4°C only one third of the ova hatched after 96 hours (17 hrs. at op. temp.) incubation at optimum temperature, and these were all dead at the end of 119 hours. Refrigeration of the ova for 82 hours at 4°C proved lethal since none developed when incubated at 33.3°C for several days.

Ova were similarly incubated at 33.3°C, and removed to 4°C at the end of 11, 34 and 59 hours. After 11 hours incubation at 33.3°C ova were equally divided between the vermiform and motile-embryo stages. Upon refrigeration for 216 hours at 4°C, these ova showed no further development. Ova which were removed from the work chamber after 34 hours at optimum temperature and were in the second larval stage, failed to develop further at 4°C, and were killed by this exposure. Ova incubated for 59 hours were equally divided between advanced second- and third-stage larvae. At the end of 170 hours refrigeration at 4°C the second-stage larvae had reached the infective stage and the entire population was normal. This illustrates conclusively that a definite critical stage had been passed by the older second-stage larvae, since these failed to succumb to the low temperature. It is apparent from these results that only advanced second-stage and infective larvae are capable of withstanding a temperature of 4°C.

EFFECTS OF HUMIDITY ON THE DEVELOPMENT OF HAEMONCHUS CONTORTUS

Very little information has been reported with reference to effects of humidity on the development of *Haemonchus contortus* ova and larvae. Veglia (1915) and Shorb (1944) discussed effects of moisture on the developing ova, but neither investigator made precise humidity studies.

Veglia (1915) merely compared development of ova and larvae in feces under three conditions. He referred to "moist feces" as being closest to that

of freshly passed fecal material, and in this he obtained the best development of both ova and larvae. "Wet feces" were described as comparable to that found in animals with diarrhea. In this medium, the ova either did not hatch, or if hatching occurred the larvae soon died. The third condition described was that called, "soaked feces" in which case the infected feces were submerged, and the ova and larvae did not survive.

Shorb (1944) performed a series of experiments to determine the degree of dryness required to kill $H._{,}$ contortus ova. He dried and pulverized feces — weighing the sample before and after subjection to 21.1-26.7°C. Distilled water then was added in an amount equal to that lost during drying. After restoration of the water, the cultures were kept about one week at room temperature to allow surviving eggs to hatch and reach infectivity. Conditions prevailing during the experiments are described by Shorb (1944) as follows: "The first experiment was made while the building was heated and the relative humidity was accordingly low. No humidity records were taken, but as the outdoor relative humidity was 49 per cent at 47°F, the calculated indoor relative humidity, if condensation and some other factors are ignored, was about 25 per cent." This author concluded that eggs of $H.$ contortus in all stages of embryonation are susceptible to the effects of desiccation.

In order to minimize as many variables as possible in the present study . preparations for the humidity experiments consisted of ova smeared upon glass slides with tap water, and exposed to circulating air in the work chamber at 33.3°C and varying relative humidities.

Ova smeared upon glass slides and exposed to 33.3°C and 100% relative humidity developed third-stage larvae in a minimum of 62 hours. Ova failed to develop in slide smears at 96% relative humidity after 62 hours exposure, and were dead when removed to water at optimum temperature as revealed by a failure to develop.

Ova failed to develop when exposed at the optimum temperature and 92% and 85% relative humidities. Similarly ova exposed to a constant relative humidity of 96% and a lower temperature (26.7°C) failed to develop.

It is apparent that $H.$ contortus ova are extremely susceptible to desiccation. It was observed that first- and second-stage larvae were extremely susceptible to drying though third-stage or infective larvae were very resistant to desiccation. Upon evaporation of the liquid medium in the dishes, the infective larvae coiled up and remained so for relatively long periods. Upon addition of water, such larvae promptly returned to normal after being dried for a maximum of four days.

EFFECTS OF CHEMICAL AGENTS ON THE DEVELOPMENT OF HAEMONCHUS CONTORTUS OVA AND LARVAE

Information concerning the effects of chemical agents on the development of *Haemonchus contortus* is very scant. Veglia (1915) sketchily reported the susceptibility of developing eggs of this species to betanapthol, thymol, picric acid and copper sulfate. After four days at 25-30°C, he reported all eggs treated with these compounds to be opaque and dead, while controls developed normally. Veglia also observed these compounds to be "injurious" to all larval stages. Swanson (1943) reported that fumigation of the soil with methyl

Table 4.—Effects of various detergents and other chemical compounds
on the ova of *Haemonchus contortus*

Chemical	% conc.	Lethal Effect
Duponol 80	(1)	m after 8.5 hrs.; no further development
	(0.1)	L1 in 33.5 hrs.; L1 subsequently killed
	(0.05)	L3 in 65 hrs.
Product J	(1)	Ovicidal in 8.5 hrs.
	(0.33)	Ovicidal in 12 hrs.
	(0.1)	me in 10 hrs.; no further development
	(0.05)	L1 in 34 hrs.; L1 subsequently killed
Santomerse D	(1)	Ovicidal in 8.5 hrs.
	(0.33)	Ovicidal in 12 hrs.
	(0.1)	m after 10 hrs.; no further development
	(0.05)	50% L1 in 34 hrs.; L1 subsequently killed
Santomerse 3	(1)	Ovicidal in 8.5 hrs.
	(0.33)	Ovicidal in 12 hrs.
	(0.1)	m after 10 hrs.; no further development
	(0.05)	me in 12 hrs.; no further development
Areskap 100	(1)	Ovicidal in 8.5 hrs.
	(0.33)	Ovicidal in 12 hrs.
	(0.1)	m after 10 hrs.; no further development
	(0.05)	L1 in 34 hrs.; L1 subsequently killed
Orvus WA	(0.33)	Ovicidal in 12 hrs.
	(0.1)	Ovicidal in 15 hrs.
	(0.05)	me in 12 hrs.; no further development
"Tergitol" 08	(1)	L1 in 17 hrs.; 50% L2 in 34 hrs.; all larvae subsequently killed
"Tergitol" 4	(1)	50% me in 11 hrs.; no further development
"Tergitol" 7	(1)	Ovicidal in 11 hrs.
"Tergitol" P-28	(1)	50% L1 in 34 hrs.; no further development
Solvent R	(0.1)	me in 12 hrs.; no further development
C-7144-C	(0.1)	me in 12 hrs.; no further development
C-1835-X-11	(0.1)	me in 12 hrs.; no further development
C-8765-CD	(0.1)	me in 12 hrs.; no further development
Betachlor	(0.1)	50% L1 in 12 hrs.; L1 subsequently killed
Propylene dichloride	(0.1)	L1 in 12 hrs.; L1 killed upon hatching
Solvent C160	(0.1)	50% L2 in 34 hrs.; L2 subsequently killed
Solvent C100	(0.1)	L3 in 82.5 hrs.
Ethylene dichloride	(0.1)	L3 in 82.5 hrs.
DDT	(1)	L1 in 17 hrs.; L1 subsequently killed
Copper sulfate	(1)	Ovicidal in 8.5 hrs.
	(0.33)	me in 12 hrs.; no further development
	(0.1)	me in 12 hrs.; no further development
	(0.05)	L1 in 34 hrs.; L1 subsequently killed
Phenol	(1)	Ovicidal in 3 hrs.
	(0.5)	m after 8.5 hrs.; no further development
	(0.33)	98% me in 12 hrs.; 2% L1 killed upon hatching
	(0.1)	L1 in 33.5 hrs.; L1 subsequently killed
	(0.05)	L1 in 34 hrs.; L1 subsequently killed

Symbols as in table 1.

bromide under paper killed all of the cattle-parasitic and free-living nematodes to a depth of at least 12 inches. *H. contortus* was included in this study.

In the first series of the present experiments, 10 and 5 percent solutions of Duponol 80, Product J, Santomerse D, Santomerse 3 and Areskap 100, killed all *H. contortus* ova within three hours as indicated by opalescent or vacuolated cytoplasm. The cytoplasm of many ova was destroyed so that only the egg shell was observable. Sterox CD and Sterox SE were ineffective in 10 percent solutions and hatching occurred in these in 9.5 hours, but the larvae died after a few hours in either of these compounds.

Further dilution of the remaining compounds (1, 0.5, 0.33, 0.1, 0.05 percent) were made until a concentration was found which permitted development of the ova beyond the morula stage. All permitted development to various stages in 0.05 percent solutions (table 4).

In addition to the above compounds, several other detergents were used in the lower concentrations (table 4). Each of these, with the exception of Orvus WA and the "Tergitol" series, was used only in 0.1 percent solutions. Orvus WA was tested in three concentrations (0.33, 0.1, 0.05 percent). The "Tergitol" compounds were tested only in 1 percent solutions.

Orvus WA in 0.33 percent solution was ovicidal in 12 hours; in 0.1 percent solution it prevented development and was ovicidal in 15 hours; in a 0.05 percent solution development was arrested at the motile-embryo stage in 12 hours. No further development occurred when the eggs removed to optimum conditions (table 4).

"Tergitol" 08 in 1 percent solution was ineffective against the ova, since first-stage larvae hatched in 17 hours, and 50% of these developed to second-stage larvae in 34 hours. All larvae were killed with subsequent exposure (table 4).

"Tergitol" 4 in 1 percent solution permitted 50% of the ova to reach the motile-embryo stage, but no further (table 4).

"Tergitol" 7 in 1 percent solution was ovicidal in 11 hours (table 4).

"Tergitol" P-28 in 1 percent solution permitted 50% of the first-stage larvae to appear within 34 hours, although there was no further development (table 4).

Solvent R, C-7144-C, C-1835-X-11 and C-8765-CD in 0.1 percent solution arrested development permanently at the motile-embryo stage in 12 hours (table 4).

Betachlor in 0.1 percent solution permitted 50% of the ova to hatch in 12 hours, although the larvae were killed upon exposure to this compound (table 4).

Propylene dichloride in 0.1 percent solution permitted all first-stage larvae to hatch in 12 hours, but these larvae were killed immediately upon hatching (table 4).

Solvent C160 in 0.1 percent permitted 50% development to the second-stage larvae within 34 hours, but these were killed in a few hours (table 4).

Solvent C100 and Ethylene dichloride in 0.1 percent solution permitted development to third-stage or infective larvae in 82.5 hours (table 4).

The most effective detergents used against *H. contortus* ova were Santomerse 3 and Arvus WA. These compounds in concentrations as low as 0.05

TABLE 5.—Effects of various chemical agents on the infective
larvae of *Haemonchus contortus*

Chemical	% conc.	Effect
Duponol 80	(1)	alive after 13 days
	(5)	killed in 20 hrs.
Areskap 100	(1)	killed in 36 hrs.
	(5)	killed in 20 hrs.
Product J	(1)	killed in 36 hrs.
	(5)	killed in 20 hrs.
Santomerse D	(1)	killed in 36 hrs.
	(5)	killed in 20 hrs.
Santomerse 3	(1)	killed in 36 hrs.
	(5)	killed in 20 hrs.
Orvus WA	(1)	killed in 36 hrs.
	(5)	killed in 20 hrs.
Copper sulfate	(1)	killed in 3 hrs..
Phenol	(1)	killed in 3 hrs.
"Tergitol" 08	(1)	alive after 13 days
	(5)	killed in 20 hrs.
"Tergitol" 4	(1)	killed in 13 days
	(5)	killed in 20 hrs.
"Tergitol" 7	(1)	killed in 16.5 hrs.
	(5)	killed in 20 hrs.
"Tergitol" P-28	(1)	alive after 13 days
	(5)	killed in 20 hrs.
Ethylene dichloride	(1)	alive after 13 days
Propylene dichloride	(1)	alive after 13 days
C-7144-C	(1)	alive after 13 days
	(5)	killed in 20 hrs.
C-8765-CD	(1)	alive after 13 days
Solvent C100	(1)	alive after 13 days
Solvent C160	(1)	alive after 13 days
Solvent R	(1)	killed after 5 days
Betachlor	(1)	coiled after 13 days
DDT	(1)	alive after 13 days

Symbols as in table 1.

percent arrested development at the motile-embryo stage, and permitted no
further development as shown in table 4.

The most effective non-detergent compounds were phenol and copper
sulfate. In a 1 percent solution of phenol, ova were killed more rapidly (3
hrs.) than in a 1 percent solution of copper sulfate (8.5 hrs.) (table 4). In
0.05 percent concentrations, phenol and copper sulfate were equally effective.

Concentrations of copper sulfate (0.05%) and phenol (0.1%) which
were not ovicidal were each combined with a non-ovicidal concentration of
Duponol 80 (0.1 percent) to observe the effects in combination with an agent
known to increase the permeability of the egg membranes. The results were
negative.

One percent DDT was not ovicidal.

It is apparent from these experiments that the ova of *H. contortus* are
relatively susceptible to many chemical agents. The minimum lethal concen-
trations of surface-active agents for *H. contortus* are far below the concentra-
tions which are injurious to *Ascaris lumbricoides* var. *suum* ova, which possess

a heavy protein coat. Concentrations showing ovicidal activity against *H. contortus* ova merely retard development of pig-ascaris ova (Thorson, 1949). The fact that *H. contortus* ova do not possess a protein coat simplifies possible control measures for this species.

Infective larvae of *H. contortus* were submerged in 1 and 5 percent solutions of various chemical agents (table 5). The most effective compounds tested in 1 percent solutions were copper sulfate and phenol, since they were larvicidal in 3 hours (table 5). "Tergitol" 7 in 1 percent solution was larvicidal in 16.5 hours. (table 5). Several other compounds (Areskap 100, Product J, Santomerse D, Santomerse 3, and Orvus WA) in 1 percent solutions killed the infective larvae within 36 hours. One compound, "Tergitol" 4, in a 1 percent solution proved larvicidal after a 13-day exposure of the larvae. The remainder of the compounds tested (Duponol 80, "Tergitol" 08, "Tergitol" P-28, Ethylene dichloride, Propylene dichloride, C-7144-C, C-8765-CD, Solvent C100, Solvent C160, Betachlor, DDT) in 1 percent solutions were not larvicidal after an exposure of 13 days at which time the experiments were terminated.

All compounds which were tested in 5 percent solutions were larvicidal within 20 hours (table 5).

SUMMARY

Velocity curves were constructed for development of *Haemonchus contortus* from the morula to infective larvae in *covered* and *uncovered* containers in tap water and feces-decoction filtrate.

The number of developmental units required to complete development from the morula to the third-stage or infective larva are 1019 and 1081, respectively, in *covered* containers of tap water and feces-decoction filtrate. These developmental units are 706 and 1074, respectively, for development in *uncovered* containers of tap water and feces-decoction filtrate.

At optimum temperature (33.3°C), *H. contortus* ova and larvae complete development to the third-stage larvae in *uncovered* containers in 60 hours in tap water or feces-decoction filtrate and in 65 hours in *covered* containers of each of these media.

Minimum lethal temperature for ova of *H. contortus* is 5.56°C. Approximately 5% of the ova hatch in 8.89°C with prolonged incubation in *covered* containers. The minimum temperature at which third-stage larvae were produced was 12.2°C but only 1% reached this stage only in the *covered* containers of feces-decoction filtrate (table 1). The minimum temperature for 100% development to the third-stage larva was 17.8°C in feces-decoction filtrate and 21.1°C in tap water in 201.5 hours and 156 hours, respectively.

The maximum temperature which permitted development to the third-stage larva was 36.7°C, but only 10% of the ova developed to this stage. This development occurred in *covered* dishes of tap water and required 132 hours. At 35.6°C all "cultures" developed 100% infective larvae in 70-80 hours.

A temperature of 37.8°C proved lethal in 5 days.

Exposure of ova at 4°C proved lethal in 82 hours. Removals from 4°C to optimum temperature (33.3°C) after exposures of 11, 34 and 59 hours showed a progressive retardation of development of infective larvae.

Ova incubated at 33.3°C and removed at 4°C at periods of 11 and 34 hours showed no further development. Ova exposed for 59 hours before removal to this temperature developed to third-stage larvae, proving that once a critical stage (advanced second-stage larva) in development is reached, development and survival of infected larvae are not inhibited by a temperature of 4°C.

Orvus WA and Santomerse 3 were the most effective surface-active agents tested against ova and larvae of *H. contortus*. They arrested development in concentrations as low as 0.05 percent. Compounds which were most effective against ova were also effective against the infective larvae.

Non-detergent chemical agents used were DDT, phenol and copper sulfate. DDT in 1 percent solutions was not ovicidal. One percent solutions of phenol and copper sulfate were ovicidal in 3 and 8.5 hours, respectively. Infective larvae were killed within 3 hours in this concentration of phenol or copper sulfate.

Ova smeared upon glass slides and exposed to relative humidities of 85, 92 and 90% at 33.3°C failed to develop. Control ova smeared upon glass slides and exposed to a relative humidity of 100% at 33.3°C developed infective larvae in 62 hours.

Ova smeared on glass slides and exposed to a relative humidity of 96% at 26.7°C failed to develop.

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The Genus Dinophilus (Archiannelida) in the United States

E. Ruffin Jones, Jr.
University of Florida, Gainesville

Frederick F. Ferguson
Puerto Rico Field Station, Communicable Disease Center Public Health Service

Because of the small size and sporadic occurrence of archiannelids, the genus *Dinophilus* has received scant attention in this country. *D. pygmaeus* was studied by Verrill in 1892 from New England, but due to the inadequacy of the description, this species must be considered invalid. *D. simplex,* another form which Verrill considered as belonging to this genus has been transferred to the turbellarian genus *Alaurina.* *D. gardineri* was studied and reported on by Moore (1899) in a preliminary note. Ruebush (1940) established the validity of this species in a careful and thorough study of material from the type locality, Woods Hole, Massachusetts. Nelson (1907) made detailed studies on a New Jersey species which he considered new and named *D. conklini.* Shearer (1912), Fauvel (1927), Hempelmann (1931) and Remane (1932) all consider *D. conklini* to be at most no more than a geographic variant of *D. gyrociliatus* Schmidt. Thus *D. gardineri* Moore and the European form *D. gyrociliatus* Schmidt (= *D. conklini* Nelson) are the only species of this genus reported from the United States. We have reported (Jones and Ferguson 1949, 1951) two other Dinophilids, *D. kincaidi*[1] from Washington on the Pacific Coast and *D. jägersteni*[2] from the Virginia-Carolina area of the Atlantic Coast, but the present paper gives the first published description of these forms.

Dinophilus kincaidi, n. sp.

figs. 1 and 2

D. kincaidi inhabits the back bay marine tidal flats of Willapa Bay, Washington. Individuals may be scooped up in great numbers along with bottom mud and shell detritus in very shallow water. Such collections may be maintained for as much as six months in laboratory aquaria with only infrequent aeration. All embryonic stages may thereby be studied. Encapsulation was not seen in our cultures, although the worms die out and reappear sporadically. Dinophilids are bottom dwellers, the adults maintaining constant activity in search of food. Young worms remain sessile until they reach a size of about 140μ in length. Half-grown animals may frequently be

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[1] Named in honor of the distinguished northwestern zoologist, Dr. Trevor Kincaid, Professor Emeritus of Zoology, University of Washington.

[2] Named in honor of Dr. Gösta Jägersten of Uppsala University, Sweden, in recognition of his extensive and painstaking work on the archiannelids.

seen moving upside down at the water surface. Food consists primarily of diatoms and algae.

Members of this species measure a little over 0.5 mm on the average and are light gray in color when not engorged with algae. They have the typical *Dinophilus* shape (fig. 1) characterized by a prominent head or prostomium and a series of poorly defined external segments. There is no indication of internal segmentation. The very young worms consist of 8 segments including the prostomium and a uniformly tiny tail appended to the last metamere. Fusion of some of these segments occurs with growth since the adult has only 6 segments (fig. 2). One region of fusion may be in the last two segments since in the adult the last segment is the only one possessing two sets of ciliary tufts.

Although we occasionally observed a structure which looked somewhat like a large flame cell and measured some 35μ in length, even with immersion of the adults in diluted sea water as suggested by Ruebush (1940), the excretory system could not be worked out. The flame cell-like structure was probably a part of the nephridial tubule.

A pair of dark red eyes is a prominent feature of the first segment. They have two retinulae each; a condition similar to that observed by Ruebush (1940) in *D. gardineri*. The brain is seen as a clear homogeneous oblong body located between the eyes.

Only female worms have developed in our cultures. Very possibly males are degenerate and inconspicuous as is the case in some species of dinophilids. The single large ovary (fig. 1, *ov*) appears in immature forms as a thickening of the ventral body wall at about the level of the intestinal-rectal juncture. It is of compact type resembling that of many simple turbellarians. Grayish-black eggs (fig. 1, *eg*) may measure as much as one-fifth of the body length. While the egg mass seems to float in the coelom it actually remains moored in a postero-ventral position. No other female apparatus is present and there is no gonopore evident.

The mouth is a heavily ciliated opening with T-shaped lips in the ventral surface of the first anterior segment.

The pharynx is a large complex ciliated structure. It is very active but is not extruded to any great extent in normal ingestion. There is a right angle bend in the organ, the greater upper part being parallel to the body axis. In the region next to the intestine there is a permanent proventriculus (fig. 1, *pv*) used for the continuous revolution of food before it is projected into the stomach-intestine. Food is injected into the intestine by means of a plunger action of the subpharyngeal proboscis (fig. 1, *pr*). Apparently hydrostatic pressure is increased in the lumen of the pharynx as the proboscis swings rapidly back and forth in a restricted arc. The bipartite proboscis is very closely attached to the ventral wall of the pharynx, its under surface swinging free in the coelom for the most part. This organ consists of a frontal lip region and a posterior bulbar part. Despite its frequently violent activity the proboscis maintains its shape. In very young worms it seems to be liquid filled and is already well developed in animals only 140μ long. Our observation of the details of construction of the proboscis agree with those of Jägersten (1947) for a Swedish species.

A pair of large, pyriform, salivary (?) glands (fig. 1, *sg*) are attached to the food revolving part of the pharynx. These glands have only a relatively few cells with large nuclei, extend posteriorly, and are present in immature stages. About 6 or 8 large greenish-brown cells are also found parallel to the pharynx. The function of these is unknown although they appear to be glandular in nature and may represent a second type of salivary gland.

The ciliated intestine (fig. 1, *in*) resembles very closely the enteron of rhabdocoelid turbellarians. It communicates via a sphincter with a thick walled ciliated rectum (fig. 1, *r*). The rectum is about one-quarter the length of the intestine and swings freely in the coelom above the ovary. There is a prominent anal sphincter controlling the external opening. The ciliated anus (fig. 1, *ap*) is actually dorsal in position since it opens onto the upper surface of the small tail.

The coelom is much reduced in size as compared with the condition in most Annelids, but there is no mesenchymal parenchyma such as is found in the acoelomate Turbellaria. The extent of the coelom in this species is similar to that described by Jägersten (1944) for a Swedish species.

The epidermis is rough and mottled in appearance due to the random disposition of banana-shaped (powder horn) glands (fig. 2, *gl*) imbedded in it which are very close in morphology to certain turbellarian rhabdite glands. They appear to be filled with large block-like granules and all have a tiny external opening visible only under oil immersion lenses. These glands occur both dorsally and ventrally and are heavily concentrated in the posterior dorsum. Epidermal cell limits are not discernible in living material.

Since epidermal ciliary patterns are of value taxonomically they will be considered in some detail. Ciliation consists of tufts of cilia (fig. 2, *ct*) (flagella?), ordinary short cilia (fig. 1, *c*) and sensory hairs (fig. 1, *sh*). When studied in methyl cellulose preparations the tufts demonstrate an undulant back and forth movement, the regular cilia have an effective beat in one direction while the sensory hairs remain rather rigid. The tactile sensory hairs are the longest of the ciliary types (up to 35μ) and are found only at the two ends of the body, distributed either singly or in small groups. The animals' venter lacks a cuticular layer and is quite evenly ciliated in a fine close set pattern. The small tail is evenly ciliated on all surfaces, otherwise the dorsum is entirely lacking in ordinary short cilia. Dorsal tufts of long cilia are arranged in rows conspicuously evident under low magnifications. They are probably the chief factors in producing rapid movement. Such tufts, which are best seen on lateral surfaces, have a definite pattern with respect to the pseudo-segmentation of the animal but it is easily understandable how taxonomic confusion has resulted from a study of the cilia-metamere relationship. As pressure of the coverslip on the worms is increased the segmentation becomes increasingly vague and ciliary activity lessens; moreover, they do not respond well to prolonged study with the methyl cellulose technique.

There are 9 sets of ciliary tufts located dorsally and laterally in the adult animal (fig. 2). The head has a V-shaped set originating between the eyes and a second set almost parallel to the first. These two sets have the same

location as the dorsally interrupted rows of short cilia in *D. gardineri*. The "neck" indentation has a row parallel to the mid-pharynx. Segments 2, 3, 4 and 5 each have single rows while 2 rows are found in segment 6. Tufts are not equatorial in segments 3, 4 and 5, but are to be found somewhat posterior to the midline. In segment 6 the anterior set is more or less complete as a row while the posterior one is always patch like and lateral in disposition. In very young individuals the 3rd segment is the most anterior to have a complete row while the rows in segments 7 and 8 are also interrupted dorsally. Young and old worms have tufts of relatively the same length. In the almost sessile young the ciliary tufts remain tightly pressed to the body and are pointed anteriorly. The control over these tufts is interesting since either single cilia or an entire tuft may be activated.

SPECIES DIAGNOSIS

D. kincaidi.—Only females known; color light gray except for gut contents, average length 0.5 mm; adult consisting of head, six trunk segments and a conical caudal appendage which is not annulated; trunk unciliated dorsally and laterally except for 9 rows of ciliary tufts arranged as followed: 2 on head, the second being interrupted dorsally, 1 on neck and 1 on each of body segments except the last which has 2 rows; ovary unpaired with very large gray eggs up to 1/5 the body length in size; resembles *D. gyrociliatus* in many respects but shows following distinguishing characteristics: 1) Ventral surface of body and entire surface of caudal appendage covered with uniform coat of small fine cilia. 2) no cuticular layer on venter; 3) banana-shaped or powder horn glands scattered; absent or almost so on head and caudal appendage, and contents of glands block like in shape; 4) no complete nephridia but only large flame cell-like structure observed in excretory system. *Type locality and only known record.*—Willapa Bay, Washington. *Holotype.* Whole mount on slide in U. S. National Museum Catalogue No. 21116. Several specimens including whole mounts and sections on slides in collection of senior author at the University of Florida, and one sectioned specimen deposited in U. S. National Museum.

Dinophilus jägersteni n. sp.

figs. 3 and 4

D. jägersteni occurs sporadically in great numbers in the shallow back waters of brackish swamps and creeks at Norfolk, Virginia and at the Duke University Biological Station at Beaufort, North Carolina. These animals are chiefly bottom dwellers moving about constantly in search of food. They swim with either their dorsal or ventral surfaces uppermost but not in a spiral path. They also move by a kind of crawling motion as they engorge protozoans and diatoms. Encapsulation which is exhibited in some species including *D. gardineri*, was not observed in laboratory cultures of this form.

These worms are visible macroscopically, measuring on the average 1.5 mm in length and are colored a deep orange brown. They have the usual shape for the genus (fig. 3). Segmentation is not evident internally and shows faintly externally only when a worm bends its body abruptly. There seem to be 7 or 8 body divisions plus a pointed tail region.

The excretory system is indistinct. We did, however, observe in some specimens what appeared to be nephridia. These numbered up to 6 on each

side and reached a length of 90μ. Presumably we did not see the entire nephridium which is probably much longer than this.

The paired orange brown eyes (fig. 3, e) consist of elongate dark masses of tiny globules with a single retinula and are located laterally in the head region near the brain. Occasionally specimens are seen with the pigment cup broken up into two sections. The brain (fig. 3, br) is a bipartite structure. There was some indication of lateral longitudinal nerves lying close to the epidermis. Nerve tissue stained pinkish in Azure II-Eosin preparations, but the nervous system did not show up well in our material.

In our early studies on this species we observed clusters of sperm in the bodies of individuals with mature ovaries. These clusters were so arranged as to resemble in appearance the testes and seminal vesicles of male individuals. This led us to conclude in a preliminary note (Jones and Ferguson, 1949) that we were dealing with hermaphroditic individuals which were protandrous and that the male system had partly degenerated in the specimens studied.

Further study has disclosed that we were in error. The sperm masses were in the coelom as a result of impregnation of the female by a male and this species, like all other known species of *Dinophilus* is dioecious not hermaphroditic. In some species of *Dinophilus* sexual dimorphism is the rule with the male being smaller in size and differing morphologically from the female. This is the case in *D. gyrociliatus* and probably also in *D. kincaidi* although the males have not been observed in this latter species. *D. jägersteni* does not show this dimorphism, however, and with the exception of the sexual apparatus there is no detectable difference between males and females, and both occur abundantly. In this respect, *D. jägersteni* resembles *D. gardineri* the species which it also most nearly resembles morphologically.

Ovaries (fig. 3, ov) are paired compact ventral organs and are very large occupying the middle two-thirds of the body in a mature female. In some specimens oocytes assume a peripheral position in the ovaries. As many as five eggs (fig. 3, eg) may be seen connected with the ovary. They are dark gray in color and have a diameter sometimes equalling one-half the body width. Nuclei stain darkish-blue in Azure II-Eosin. A female gonopore seems to be lacking. While animals in cultures constantly lay eggs their method of releasing the egg from the body was not ascertained. In the male the testes (fig. 4, t) are paired and lateral in position and are elongate slightly indented compact organs. Testes may originate lateral to the pharynx and extend to the beginning of the rectum. In fully mature individuals they commonly coalesce or fuse ventrally. Living sperm cells are undifferentiated colorless undulant ribbons measuring about 75μ in length. The penis (fig. 4, p) is a conical structure with a muscular sheath. The upper region is a glandose prostate or granular vesicle provided with paired sets of glandular rosettes. The blunted tip of the penis is covered with a somewhat hardened or stiffened tunic. The male organ is about 75μ long and lies ventral to the vesicula seminalae (fig. 4, vs). No male genital atrium is visible. The male gonopore (fig. 4, mg) is a distinctly visible ciliated ventral opening just posterior to the anus and is about 75μ from the posterior tip of the tail. Paired seminal vesicles connect with short sperm ducts which communicate with the penis. The vasa deferentia (fig. 4, vd) are usually quite prominent.

Copulation occurs between male and female worms with the male organ applied (hypodermically?) at random to the body surface of the female. Fertilization takes place in the coelom and the fertilized eggs are soon released from the body to continue their development in the water.

The mouth (fig. 3, *m*) is a ciliated opening in the ventral surface of the head segment. The ciliated pharynx has a right angle bend and is intimately attached to the sub-pharyngeal proboscis (fig. 3, *pr*) so well described by Jägersten (1947), in other species. The pharynx is well supplied with eosinophilic gland cells. The proboscis is roughly bipartite and consists of a series of muscle cell plates enclosed in a tunic of connective tissues. The pharynx leads into an upper esophageal region which is separated from the intestine by a distinct sphincter. Extensive blind sacs extend anteriorly from the densely ciliated intestine (fig. 3, *in*). In the roof of the anterior intestine there are large single celled glands which are somewhat reminiscent of the chlorogogue cells in the typhlosole of earthworms. Stubby columnar cells form an epithelial lining which is thickest in the ventro-posterior region of the intestine and continues into the rectal chamber. The rectum (fig. 3, *r*) arises from the dorsal posterior wall of the midgut or intestine from which it is separated by a well developed sphincter. It is always displaced slightly to the left of the midline whereas in *D. gardineri* it is median in position. The ciliated epithelium of the rectum is non-vacuolate and thinner than that of the intestinal lining, but the difference in the thickness of the gut wall in these two regions is not so pronounced as *D. gardineri*. A well developed anal canal extends from the rectum to the anal pore (fig. 3, *ap*) which is dorsal in position and lies near the base of the caudal appendage. The coelom is similar to that of *D. kincaidi* and other dinophilids and coelomic space is quite limited.

This species is unique in the genus in so far as the arrangement of epidermal cilia is concerned. With the exception of *D. gardineri* all species of *Dinophilus* have one or more ciliary bands or rings in each segment of the body. *D. gardineri* has only scattered tufts of cilia on the trunk but has two bands or rings on the head. *D. jägersteni* has scattered tufts over the entire body surface with no bands or rings even on the head. The cilia are much shorter and the tufts thicker and more numerous on the ventral surface than elsewhere. Tufts of sensory hairs are also widely scattered over the body in *D. jägersteni* whereas in *D. gardineri* they appear to have a definite arrangement and distribution.

SPECIES DIAGNOSIS

D. jägersteni.—Color dull orange brown—average length 1.5 mm; body with head trunk and tail probably representing 7 to 8 segments, but segmentation indistinct, no ciliary bands but ciliary tufts scattered over entire body surface; tufts of sensory hairs also scattered over body; male system like that of *D. gardineri* but with testes often fusing ventrally and with male atrium not differentiated; penis with slightly hardened, cuticular tunic; male gonopore ventral just posterior to dorsal anus; female with large paired ventral ovaries and no accessory organs or gonopore; no sexual dimorphism. *Type locality.*—Marsh, foot of Cornwall Street, Norfolk, Virginia. *Distribution.*—Found commonly around the Norfolk area and also in the vicinity of Beaufort, North Carolina. *Holotype.*—One specimen sectioned transversely deposited in U. S. National Museum, Catalogue No. 21117. Also two slides including one whole mount; one pair in copula deposited in U. S. National Museum Catalogue No. 21117.

LEGENDS FOR FIGURES

ap—anal pore; br—brain; c—cilia; ct—ciliary tufts; e—eyes; eg—eggs; gl—epidermal gland; in—intestine; m—mouth; mg—male gonopore; ov—ovary; p—penis; pr—pharyngeal proboscis; pv—proventriculus; r—rectum; sd—spermatic duct; sg—salivary gland; sh—sensory hairs; sp—sphincter; t—testes; vd—vas deferens; vg—vesicula granulorum; vs—vesicula seminalis.
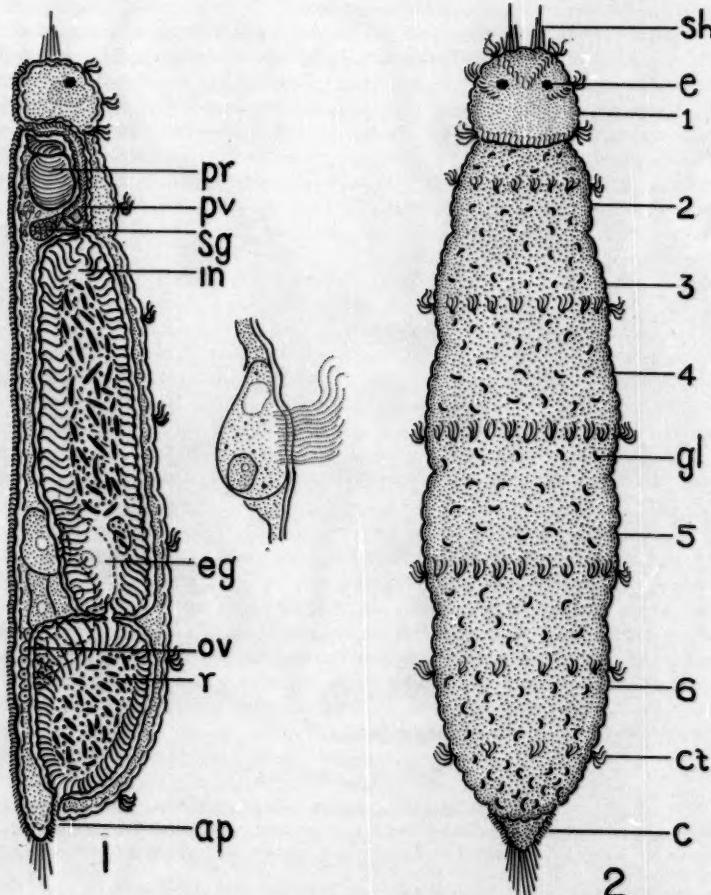
Figs. 1, 2.—*D. kincaidi.* 1. Optical section of lateral view showing internal organs (×240). Detail shows origin of cilia. 2. Dorsal view showing segmentation and ciliation (×240).
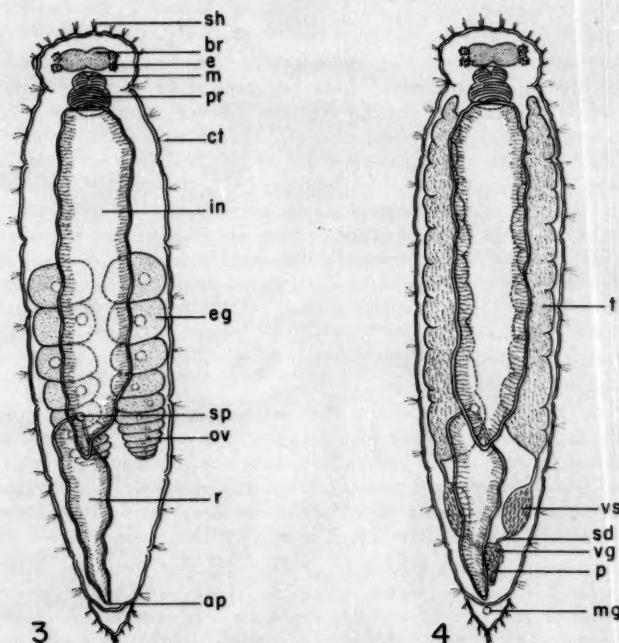
Figs. 3, 4.—Dorsal view of *D. jägersteni*. 3. Female (×65); 4. Male (×65).

DISCUSSION

The problems of species differentiation and nomenclature are particularly troublesome in the Archiannelida. This is due at least in part to the inadequacy of the descriptions in many cases. Because of this difficulty some workers have refrained from using scientific names for forms which they have studied. Thus Schimkewitsch (1895) refers to his form as "*Dinophilus* from the White Sea" and Jägersten (1944) who made a very thorough and comprehensive study of a Swedish form simply calls it "*Dinophilus* from Sweden." The work of these men and particularly that of Jägersten on the archiannelids has been outstanding and it seems that they certainly should be able to decide what constitutes a new species of this genus. We have, however, had an opportunity which apparently they have not, of comparing our Atlantic Coast form, *D. jägersteni*, with *D. gardineri* the species which it most resembles morphologically.

The senior author during several summers at the Marine Biological Laboratory, Woods Hole, Massachusetts collected a great many individuals of *D. gardineri*. These were studied in the living condition and by means of sections and there are definite morphological differences between the Woods Hole form and the Virginia-Carolina form. Furthermore, encapsulation

which occurred readily in *D. gardineri* was not observed in laboratory cultures of *D. jägersteni* indicating that these two forms may also differ physiologically.

Morphologically the Pacific Coast form is closest to *D. gyrociliatus*. We did not have an opportunity to study specimens of *D. gyrociliatus* and have, therefore, had to depend upon the literature for our knowledge of this form. This is one of the better known species of the genus and several other forms which have been described as distinct species are considered by various workers (Shearer 1912, Fauvel 1927, Hempelmann 1931, Remane 1932) to be either identical with or no more than geographic variants of *D. gyrociliatus*. While *D. gyrociliatus* and most of these variants are known only from European waters, *D. conklini* Nelson from the Atlantic Coast of the United States is also considered by these authors to be a geographical variant of *D. gyrociliatus*. The Pacific Coast *Dinophilus* which we have studied differs in various ways from *D. gyrociliatus* and from all of its variants. Further, none of the *D. gyrociliatus* group has been reported from the Pacific so far as we have been able to determine.

While it is quite conceivable that we may be dealing with geographic variants as Jägersten believes that he and various other workers may also have done; nevertheless, in view of the facts cited, it seems advisable to us to give these forms specific rank. When the morphology, geographic distribution, and interbreeding potentialities of these various populations are better known it may be necessary to re-examine this question.

We found these three species, *D. gardineri, D. jägersteni,* and *D. kincaidi,* in abundance in their respective habitats and have had literally hundreds of individuals of each species available for study. It occurred to us that one reason for the lack of knowledge of archiannelids was that they were generally overlooked because of their small size, sporadic occurrence, and secretive habits and that careful collection would demonstrate a wide distribution for them. The senior author during the past eight years has made numerous attempts to find archiannelids along the Florida Coast. Collections have been made along both the Atlantic and Gulf Coasts and many Turbellaria have been observed but no archiannelids. We still feel that they must be here and that sooner or later they will be found, but apparently it is not as simple a matter as we at one time thought.

SUMMARY

Two new species of the archiannelid genus *Dinophilus* are described. Females of *D. kincaidi* were found in abundance in the tidal flats of Willapa Bay, Washington, but no males were observed. Nor did males appear in laboratory aquaria where worms were maintained alive for six months. This is the first archiannelid reported from the Pacific Coast of the Americas and the first dinophilid from anywhere in the Pacific so far as we know. *Dinophilus jägersteni* is the third archiannelid species to be reported from the Atlantic Coast of North America and all three are dinophilids. This species occurs in abundance in the vicinity of Norfolk, Virginia, and Beaufort, North Carolina.

It is probable that archiannelids are much more common and widely dis-

tributed than is generally realized. However, repeated collections along both
the Atlantic and Gulf Coasts of Florida have failed to produce any archian-
nelids in this area to date.

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Mites Found on Mice of the Genus Peromyscus in Utah. III. Family Dermanyssidae[1]

Dorald M. Allred[2]

University of Utah, Salt Lake City

In two previous papers (Allred, 1956 a and b), the author discussed the background of the present study. This paper presents data on eight species of mites of the family Dermanyssidae found on mice belonging to five species of *Peromyscus, P. boylii, P. crinitus, P. eremicus, P. maniculatus,* and *P. truei,* over a period of five years in Utah. Two species are described as new.

ORNITHONYSSUS BACOTI (Hirst), 1913

Figs. 69-74

The type specimens were collected from "rats" in Egypt. This species is known to occur in Australia, Europe and North America. Although it has been collected most frequently from the Norway rat, *Rattus norvegicus,* infrequent collections have been made from other rodents. In Utah, this species probably is state-wide in distribution. It has been collected at elevations between 2500 and 7000 feet, principally in the Upper Sonoran Life-zone.

In this study, 25 females, 4 males and 47 nymphs were collected from 24 mice during the period from May through September. The largest numbers were found in July.

Six of the 24 times that it was collected, *O. bacoti* was the only mite found on its host. At other times, it was associated with the following species the numbers of times indicated: *Haemolaelaps glasgowi,* 6; *Trombicula montanensis,* 2; *Eulaelaps* sp., 1; *Eubrachylaelaps debilis,* 3; *E. hollisteri,* 1; *E. circularis,* 3; *Dermanyssus* sp., 6; *Hirstionyssus* sp., 2; *Ischyropoda armatus,* 1; Eremaeidae, 1.

Dermanyssus becki, n. sp.

Figs. 1-18, 74

Female.—The lengths of the idiosomas of ten engorged specimens vary from 955 to 1139 microns, average 1058; length of the holotype is 984. The widths of the idiosomas of ten engorged specimens vary from 632 to 867 microns, average 755; width of the holotype is 676.

The dorsal plate is entire and less than one-half as wide as the dorsum; it is narrowed posteriorly, slightly concave near the posterior end, and terminates in a rounded point; there are 13 pairs of setae, some barbed, some smooth; the anterior setae are larger than the posterior setae. The setae on the unsclerotized portion of the dorsum are barbed.

The sternal plate is moderately concave on the posterior border and slightly concave on its anterior edge; it has three pairs of smooth setae and two pairs of pores. The genitoventral plate tapers posteriorly, ends in a blunt point, and has one pair of smooth

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[1] A portion of a thesis submitted to the University of Utah in partial fulfillment for the degree of Doctor of Philosophy.

[2] Now at Brigham Young University, Provo, Utah.
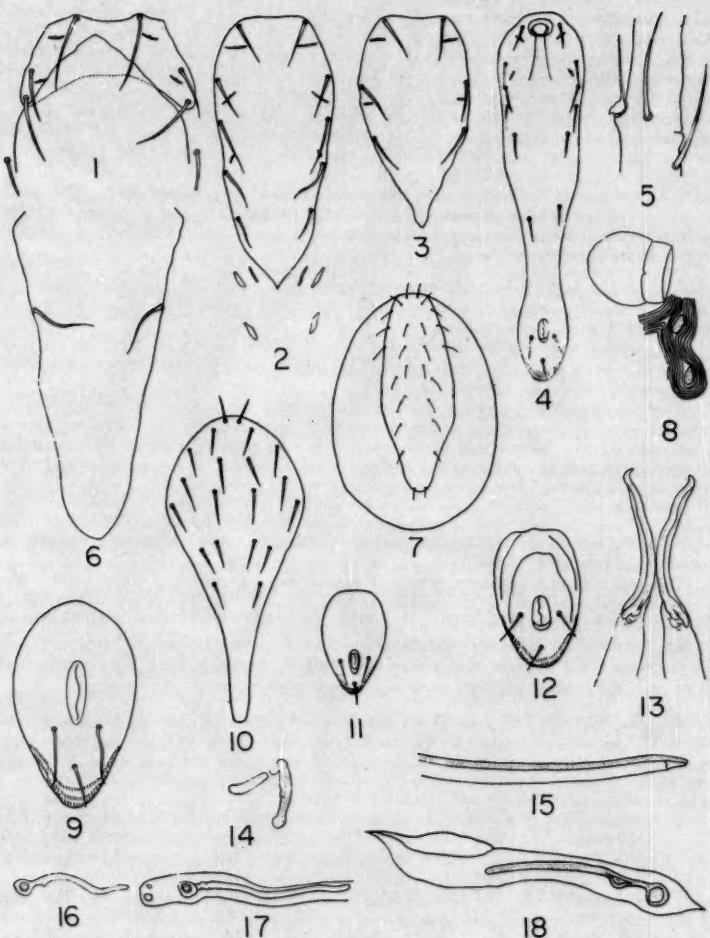
Figs. 1-18.—*Dermanyssus becki.* 1. Sternal plate and overlapping, anterior end of genitoventral plate of female; 2. Sternal plate and accessory plates of deutonymph; 3. Sternal plate of protonymph; 4. Holoventral plate of male; 5. Ventral view of left tarsus III and specialized seta of male; 6. Genitoventral plate of female; 7. Dorsal plate of female; 8. Left coxa IV and metapodal plates of deutonymph; 9. Anal plate of female; 10. Dorsal plate of protonymph; 11. Anal plate of protonymph; 12. Anal plate of deutonymph; 13. Ventral view of chelicerae of male; 14. Right peritreme of protonymph; 15. Chelicera of female; 16. Right peritreme of male; 17. Right peritreme of female; 18. Left peritreme of deutonymph.

setae; the anterior end is sharply pointed and overlaps the sternal plate. The anal plate is egg-shaped with a bluntly-pointed anterior end. The anus is three times as long as wide, and situated behind the anterior edge of the plate by a distance about equal to the length of the anus. The paired anal setae are situated opposite the posterior border of the anus. The unpaired seta forms an approximate equilateral triangle with the paired setae. All anal setae are smooth. The antero-medial setae on the unsclerotized portion of the venter are smooth; the lateral and posterior setae are barbed. There are two pairs of metapodal plates of about equal size, similar in shape in adult males and females and in the deutonymphs, but more widely separated in the females. The peritreme ends slightly posterior to the middle of coxa II.

All legs are of about equal size and possess smooth and barbed setae. The gnathosomal and palpal setae are smooth. The chelicerae are very thin and elongate with minute terminal chelae. There is a thickened, sclerotized ridge which extends almost the entire length of the immoveable chela.

Male.—The body is broadest anteriorly and tapers posteriorly to a blunt point. The lengths of the idiosomas of two males are 823 and 838 microns. The widths at the widest point are 603 and 571 microns.

The narrow, dorsal plate is entire and resembles the holoventral plate in shape and size; it has seven pairs of smooth setae. The barbed setae on the unsclerotized portion of the dorsal surface are sparsely arranged.

The holoventral plate, which is entire and encloses the anterior genital opening and posterior anus, is almost twice as broad anteriorly as posteriorly; the lateral margins are moderately concave just anterior to the anus; it has six pairs of smooth setae in addition to the regular anal setae; the paired anal setae are situated near the posterior end of the anus, and the unpaired seta forms an equilateral triangle with the paired setae. The setae on the unsclerotized portion of the venter are sparsely located; some are smooth and some barbed. There are two pairs of metapodal plates of equal size similar to those of the adult female and deutonymph. The peritreme is slightly curved, elbowed anteriorly, and extends to the anterior edge of coxa III.

The legs are of about equal size and possess some smooth and some barbed setae. There is a specialized seta at the middle of tarsi III and IV. The length-width ratios of the tarsi are: I, 4.3:1; II, 4:1; III, 4.2:1; IV, 6.6:1.

All gnathosomal setae are smooth. The chelicerae are modified for sperm transfer; the moveable chela is moderately sclerotized, elongate, curved and slightly hooked on the distal end; the immoveable segment is lightly sclerotized, curved and flattened.

Deutonymph.—The lengths of the idiosomas of eight engorged specimens vary from 514 to 852 microns, average 718. The widths vary from 396 to 661 microns, average 531.

The dorsal plate is entire and has 13 pairs of setae. The size and shape of the plate and the setal arrangement are similar to the adult female. The dorsal setae are not as large as on the adult female and are fewer in number.

The ventral plate is sharply pointed posteriorly and almost truncate anteriorly; it has five pairs of smooth setae and three pairs of pores. There are three pairs of small accessory plates near the posterior end of the ventral plate. The anal plate is oval, and the anterior end is almost truncate with a small, median hump. The anus is twice as long as wide; it is situated behind the anterior edge of the plate by a distance of twice the length of the anus. The paired anal setae are at a level with the middle of the anus. The unpaired seta forms an approximate equilateral triangle with the paired setae. All anal setae are smooth. The ventral setae are not as large as on the adult female and are fewer in number. The two pairs of metapodal plates are similar in shape to those of the adult female but are closer together and slightly smaller. The peritreme is relatively short and extends to the anterior edge of coxa III. The legs, chelicerae and gnathosomal setae are similar to those of the adult female.

Protonymph.—The lengths of the idiosomas of eight engorged specimens vary from 529 to 984 microns, average 806. The widths vary from 350 to 735 microns, average 576.

The dorsal plate is entire with the posterior end strongly constricted and finger-like; there are 10 pairs of setae. The dorsal setae are more slender and fewer in number than on the deutonymph.

The ventral plate tapers gradually to a posterior point; it has three pairs of smooth

setae. The anal plate is egg-shaped with a slightly truncate anterior end. The anus is twice as long as wide, situated behind the anterior edge of the plate by a distance of two and one-half times the length of the opening. The paired anal setae are on a level with the middle of the anus. The unpaired seta forms an equilateral triangle with the paired setae. All anal setae are smooth. The ventral setae are more slender and fewer in number than on the deutonymph or adult female. There is only one pair of metapodal plates. The peritreme is very short, and appears to consist of two or three parts. It barely extends past the posterior edge of coxa III. The legs, chelicerae and gnathosomal setae are similar to the deutonymph.

Type material.—The female holotype and male allotype were collected from an adult female *Peromyscus eremicus* at Toquerville, Washington County, Utah by the author on September 5, 1951. There are two females on the slide containing the holotype. The holotype has the chelicerae curved over right leg I. Five protonymph, six deutonymph and one female paratypes were collected from the same mouse as the holotype and allo-type. Twelve protonymph, 25 deutonymph, one male and eight female paratypes were collected from *Peromyscus boylii* from San Juan County, *Peromyscus crinitus* from Millard, San Juan, Wayne and Washington counties, *Peromyscus eremicus* from Washington County, and *Peromyscus maniculatus* from Boxelder, San Juan and Washington counties. The holotype, allotype and some paratypes are in the collection of the United States National Museum. Other paratypes are deposited in the collections of the author; Dr. F. da Fonseca, Instituto Butantan, Sao Paulo, Brazil; Museum National d'Histoire Naturelle; Natal Museum; British Museum Natural History; and University of Utah.

With one exception, the known distribution of this species in Utah is southern. It was collected at elevations between 2500 and 5000 feet, principally in the Upper Sonoran Life-zone.

Eleven females, two males and 47 nymphs were collected from 20 mice during the period from May through September except for two collections in December in southern Utah. Female mites were collected in July, August, September and December; males in July and September; and nymphs from May through September and in December. The greatest numbers of mites were found in September.

Six of the 20 times that it was collected, *Dermanyssus becki* was the only mite found on its host. At other times, it was associated with the following species the numbers of times indicated: *Eubrachylaelaps hollisteri,* 2; *E. circularis,* 1; *E. debilis,* 1; *Ornithonyssus bacoti,* 1; *Hirstionyssus* sp., 4; *Haemo-*

TABLE 1.—Check-list and host correlation of the numbers and kinds of mites of the family Dermanyssidae taken from each of five species of *Peromyscus*

No. of mice examined	No. of mites taken from each species of *Peromyscus*							
	Ornithonyssus bacoti	*Dermanyssus becki*	*Hirstionyssus femuralis*	*H. geomydis*	*H. hilli*	*H. incomptus*	*H. isabellinus*	*H. occidentalis*
Peromyscus boylii (37)	1	1						
P. crinitus (67)	1	12				2		6
P. eremicus (201)	2	43	1		7			1
P. maniculatus (2907)	61	4		2	2	5	1	409
P. truei (59)	11							

laelaps glasgowi, 3; *Brevisterna utahensis*, 1; *Ischyropoda armatus*, 1; *Hypo-aspis* sp., 1; Parasitidae, 1; Pachylaelaptidae, 1.

Hirstionyssus femuralis, n. sp.

Figs. 27-35, 74

Body.—The oval idiosoma is 602 microns long and 367 wide. The dorsal plate is drop-shaped, covers about one-half the dorsal surface of the body, has slightly convex antero-lateral margins, 25 pairs of setae and 16 pairs of pores.

Venter.—The length of the sternal plate in the center is equal to one-half the distance between the third sternal setae; it has three pairs of smooth setae and two pairs of small pores; the latero-posterior angles are extended and pointed. The posterior end of the genitoventral plate is broadly rounded; it has two slight convexities situated at a point just posterior to the single pair of genitoventral setae. The anal plate is somewhat egg-shaped, with the postero-lateral margins slightly concave. The anus is situated in the anterior half of the plate. The paired anal setae are situated slightly anterior to a point opposite the middle of the anus. The unpaired seta is located at a distance greater than its length behind the anus. The peritreme extends anteriorly to the middle of coxa I. There are approximately 14 pairs of setae on the unsclerotized portion of the venter.

Legs.—Legs II are larger than the others. Legs I are larger than legs III and IV which are of about equal size. Coxa II has three spurs and two setae; the latero-caudal spur is short and blunt; the inner spur is elongate and blunt and directed at a right angle from the distal edge of the coxal segment; the anterior spur is elongate and more sharply pointed than the other spurs. Femur II has a small, blunt spur on its anterior margin; a modified seta which has a swollen base and tapers abruptly to a sharp point is located near this spur. Two modified setae which resemble two blunt spurs occur near the distal end of tarsus II; on the anterior edge of the segment there are two modified setae which have their bases conspicuously swollen on one side. Coxa III has two spurs; the inner spur is bluntly pointed and about four times as large as the posterior spur. Length-width ratios of the tarsi are: I, 3:1; II, 2.3:1; III, 3:1; IV, 3.7:1.

Type Material.—The female holotype (containing one egg) was collected from a female mouse of the genus *Peromyscus* (probably *P. eremicus*), one-half mile west of Rockville, Washington County, Utah, December 18, 1950 by D E. Beck and D. M. Allred. The holotype is in the collection of the United States National Museum.

Discussion.—This species is so named because of the distinctive structure of femur II. The latero-caudal projection of coxa II places this species with the *Hirstionyssus tricanthus*, *H. hilli* and *H. geomydis* group. The stout modified setae of tarsus II relates *H. femuralis* and *H. geomydis*. The modified setae of tarsus II, the spurs and setae of femur II, coxae II and III, and the shape of the sternal plate readily separate *H. femuralis* from other species.

HIRSTIONYSSUS GEOMYDIS (Keegan), 1946

Figs. 36-43, 74

Keegan (1946) described *H. geomydis* from two females and one male taken from a pocket gopher, *Geomys bursarius*, from Kansas. The mites collected in this study differ from Keegan's description. His drawing of the sternal plate shows a concave posterior margin. In the specimens from Utah, the posterior margin of the sternal plate is convex, and is slightly more than half as long as it is broad. The anal plate is more egg-shaped than triangular. Keegan illustrated the spurs on coxa III as being of about equal size and
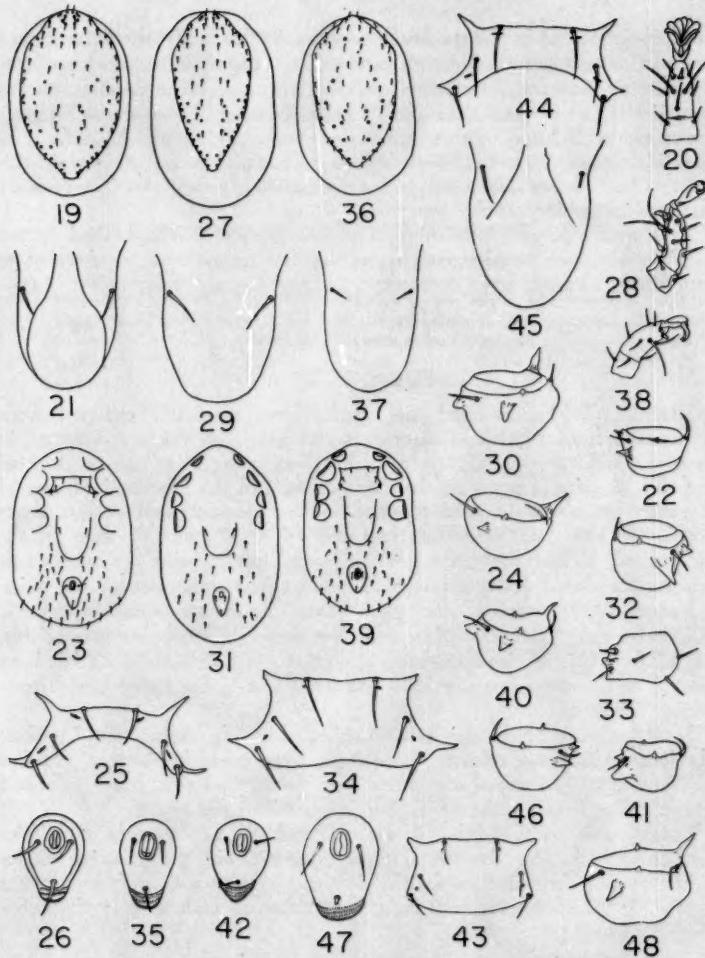
Figs. 19-48—19-26. *Hirstionyssus occidentalis.* 19. Dorsal plate of female; 20. Ventral view of right tarsus II of female; 21. Genitoventral plate of female; 22. Ventral view of right coxa III of female; 23. Arrangement of ventral setae of female; 24. Ventral view of right coxa II of female; 25. Sternal plate of female; 26. Anal plate of female. 27-35. *Hirstionyssus femuralis.* 27. Dorsal plate of female; 28. Lateral view of left tarsus II of female; 29. Genitoventral plate of female; 30. Ventral view of right coxa II of female; 31. Arrangement of ventral setae of female; 32. Ventral view of left coxa III of female; 33. Ventral view of left femur II of female; 34. Sternal plate of female; 35. Anal plate of female. 36-43. *Hirstionyssus geomydis.* 36. Dorsal plate of female; 37. Genitoventral plate of female; 38. Ventro-lateral view of right tarsus II of female; 39. Arrangement of ventral setae of female; 40. Ventral view of right coxa II of female; 41. Ventral view of right coxa II of female; 25. Sternal plate of female; 26. Anal plate of female. 44-48. *Hirstionyssus isabellinus.* 44. Sternal plate of female; 45. Genitoventral plate of female; 46. Ventral view of left coxa III of female; 47. Anal plate of female; 48. Ventral view of right coxa II of female.

sharply pointed, but in the specimens collected in this study, the internal spur is much enlarged and rounded. Keegan did not mention the presence of the two modified setae on the terminal part of tarsus II. The dorsal plate has approximately 24 pairs of setae and 13 pairs of pores. Inasmuch as Keegan's type specimen is lost (Strandtmann, correspondence), it will be difficult to determine the exact taxonomic placement of the two mites collected in this study. Until further collections and study can clarify their position, they are tentatively determined as *H. geomydis*.

This species has been taken from pocket gophers in the United States. In this study, two females were found on two *Peromyscus maniculatus* at Steep Creek, 12 miles north of Boulder, Garfield County, July, 1953.

HIRSTIONYSSUS HILLI (Jameson), 1950

Figs. 49-56, 74

Jameson (1950) described this species from specimens collected from pocket mice from Nevada, California and Kansas. Specimens collected in this study in Utah vary slightly from his description; there are 28 pairs of setae and 18 pairs of pores on the dorsal plate, and the unsclerotized part of the venter has about 15 pairs of setae. The type specimens possess about 25 pairs of setae on the dorsal plate and 16 or 17 pairs of setae on the unsclerotized part of the venter. Jameson did not mention the number of pores on the dorsal plate, although his illustrations show nine or ten pairs.

Keegan (1953) reported this species from the kangaroo rat, *Dipodomys ordii*, wood rat, *Neotoma lepida*, and deer mouse, *Peromyscus maniculatus*, from Utah. This species apparently is southern in distribution. It has been collected at elevations between 2500 and 5000 feet in the Lower and Upper Sonoran life zones.

Type specimens of this species were collected in July, August and October; collections from Utah reported by Keegan were made in August, October and November. In this study, mites were found in April, May, July and August. One female collected in August contained one egg.

Two of the five times that it was collected, *H. hilli* was the only mite found on its host. At other times, it was associated with the following species the numbers of times indicated: *Hirstionyssus occidentalis*, 2; *Haemolaelaps glasgowi*, 1; *Euschongastia criceticola*, 1; *Brevisterna utahensis*, 1; *Eubrachylaelaps hollisteri*, 1.

HIRSTIONYSSUS INCOMPTUS (Eads and Hightower), 1952

Figs. 57-68, 74

Eads and Hightower (1952) named this species from specimens collected from kangaroo rats and pocket mice from Texas. Mites collected in this study in Utah are similar to the description of the type. In Utah, this species probably is state-wide in distribution. It has been collected at elevations between 3000 and 5000 feet, principally in the Upper Sonoran Life-zone.

Seven females were collected from four mice. The infrequency of occurrence of this species on mice of the genus *Peromyscus* indicates that the infes-

tations were accidental. Type specimens of this species were collected in
January, March and April. In this study, mites were collected in May, June
and August. Two females collected in May and August each contained
one egg.

Other species that were found on the same hosts with *H. incomptus* are
Brevisterna utahensis, *Haemolaelaps glasgowi*, *Eubrachylaelaps debilis* and
Ornithonyssus bacoti.

HIRSTIONYSSUS ISABELLINUS (Oudemans), 1913

Figs. 44-48, 74

Oudemans described *H. isabellinus* from specimens collected from animals
of the genus *Mustela* from Holland. Fonseca (1948) reported this species
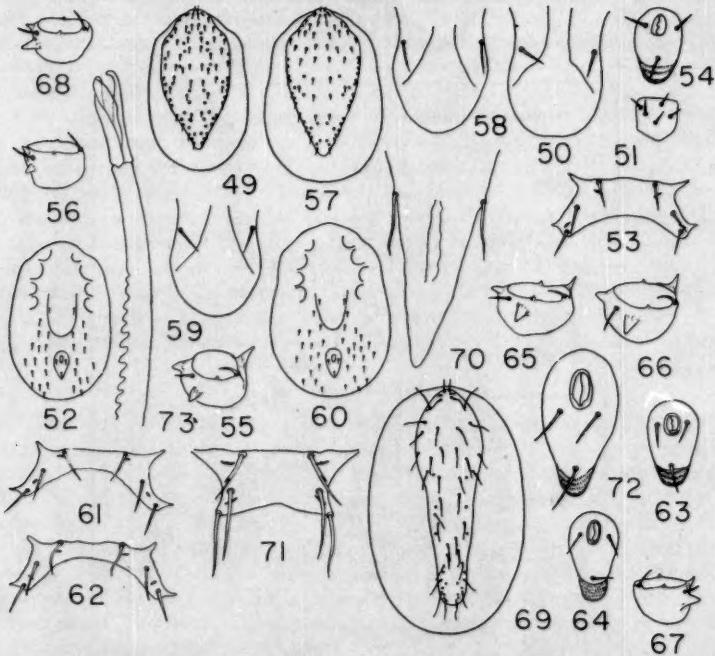
Figs. 49-73.—49-56. *Hirstionyssus hilli.* 49. Dorsal plate of female; 50. Genito-
ventral plate of female; 51. Ventral view of left femur II of female; 52. Arrangement of
ventral setae of female; 53. Sternal plate of female; 54. Anal plate of female; 55. Ventral
view of right coxa II of female; 56. Ventral view of right coxa III of female. 57-68.
Hirstionyssus incomptus. 57. Dorsal plate of female; 58, 59. Genitoventral plate of
female; 60. Arrangement of ventral setae of female; 61, 62. Sternal plate of female; 63,
64. Anal plate of female; 65, 66. Ventral view of right coxa II of female; 67. Ventral
view of left coxa III of female; 68. Ventral view of right coxa III of female. 69-73.
Ornithonyssus bacoti. 69. Dorsal plate of female; 70. Genitoventral plate of female;
71. Sternal plate of female; 72. Anal plate of female; 73. Ventral view of chelicera of
female.

from animals of the genera *Mustela, Talpa, Paludicola* and *Mus* from Europe, a mouse from Columbia, and a mole, *Scapanus* sp., from Oregon in the United States. Keegan and Hedeen (1952) reported *H. isabellinus* from animals of the genera *Lemmus* and *Microtus* from Alaska.

In this study, a single female was taken from a *Peromyscus* sp. at Steep Creek, 12 miles north of Boulder, Garfield County in July, 1953. Mites of the species *Haemolaelaps glasgowi* and *Listrophorus* sp. were found on the same host with *H. isabellinus*.

HIRSTIONYSSUS OCCIDENTALIS (Ewing), 1923

Figs. 19-26, 74

Ewing (1923) described this species from two female mites taken from squirrels of the species *Sciurus hudsonicus richardsoni* from Montana. The description of the type is somewhat general and lacks adequate illustrations.

⊞ O. BACOTI	⊙ H. HILLI
◔ D. BECKI	● H. INCOMPTUS
◼ H. FEMURALIS	◰ H. ISABELLINUS
◪ H. GEOMYDIS	⊡ H. OCCIDENTALIS
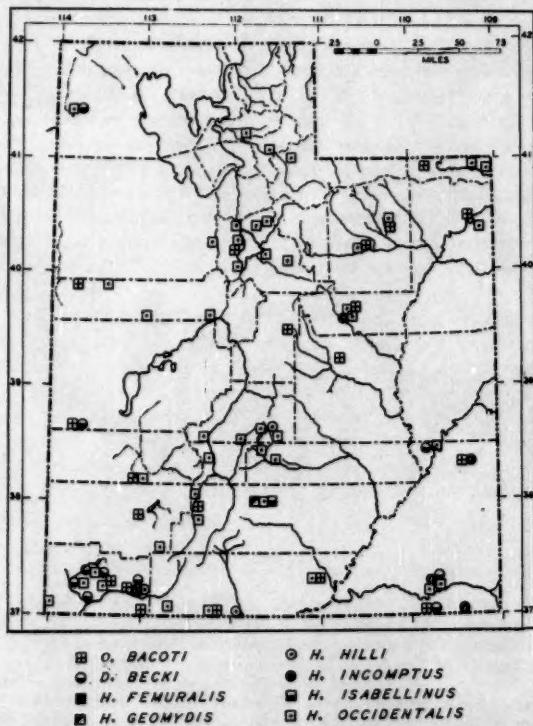
Fig. 74.—Collection localities of *Ornithonyssus bacoti, Dermanyssus becki, Hirstionyssus femuralis, H. geomydis, H. hilli, H. incomptus, H. isabellinus,* and *H. occidentalis* in Utah.

In Jameson's (1950) key to the species of *Hirstionyssus*, the mites collected in this study fit in the *H. carnifex*, *H. occidentalis* and *H. affinis* group. There is some question as to whether these mites are *H. carnifex* or *H. occidentalis*. However, on the basis of Ewing's description of *H. occidentalis*, and opinions of Strandtmann and Jameson (correspondence), these specimens are tentatively determined as belonging to *H. occidentalis*.

Hirstionyssus occidentalis has been collected from tree squirrels of the genus *Tamiasciurus* in western United States. In Utah, this species is state-wide in distribution. It has been collected at elevations between 2500 and 10,000 feet in all the life zones from the Lower Sonoran to the Canadian, most frequently in the Upper Sonoran.

Two males, 402 females and 12 nymphs were collected from 261 mice during the period from February through October. The greatest numbers were taken in March, May, June and August. Only four of 394 mites examined each contained one egg; these were collected in July and October. Female *Peromyscus maniculatus* had an average infestation of mites twice as great as the male mice.

Forty-three of the 261 times that it was collected, *H. occidentalis* was the only mite found on its host. At other times, it was associated with the following species the numbers of times indicated: *Hirstionyssus hilli*, 2; *H. isabellinus*, 1; *Eubrachylaelaps circularis*, 5; *E. debilis*, 14; *E. hollisteri*, 1; *Euschongastia criceticola*, 10; *Dermanyssus becki*, 3; *Haemolaelaps glasgowi*, 34; *H. megaventralis*, 4; *Rhizoglyphus echinopus*, 1; *Laelaps nuttalli*, 1; *Brevisterna utahensis*, 1; *Hypoaspis leviculus*, 2; *Eulaelaps* sp., 1; *Listrophorus* sp., 1; *Ischyropoda armatus*, 4; *Euhaemogamasus* spp., 2; *Garmania* sp., 1; *Radfordia* sp., 1; Pyemotidae, 1; Tetranychidae, 1; Ascaidae, 1; Pachylaelaptidae, 1; Gamasolaelaptidae, 1; Parasitidae, 2; Laelaptidae, 5.

DISCUSSION

Allred (1956b) pointed out that mites of several species in Utah are generally restricted to certain faunal areas. *Dermanyssus becki* is generally southern in distribution, and probably extended its range northward into Utah via the Virgin River and Colorado River drainages. Apparently, it is restricted almost entirely to these areas in Utah. Although not host specific, this species is associated much more frequently with *Peromyscus crinitus* and *P. eremicus* than with the other three species of mice on which it was found. However, the known range of this mite does not correspond entirely with that of one of its "preferred" *Peromyscus* hosts. This may indicate a preferred host other than a white-footed mouse.

The abundance of *Hirstionyssus occidentalis* on *Peromyscus maniculatus* and *P. crinitus* indicates a common association. It is likely that these mice are the preferred hosts of this mite, for the distribution of *H. occidentalis* corresponds with the ranges of these two species of mice. Although *H. occidentalis* apparently is state-wide in distribution, it was not found on white-footed mice between north latitudes 38 degrees 38 minutes and 39 degrees 34 minutes. The reason for this is unknown, for considerable collecting was done in that area.

Ornithonyssus bacoti is not host specific on any one of the white-footed

mice, for it was found on all five species. However, it apparently prefers *P. truei* over the others.

Although they are not uncommon on white-footed mice, mites of the other species of *Hirstionyssus* collected apparently do not utilize these mice as their preferred hosts. Nevertheless, in all cases it is possible that mites of these species are primarily nest dwellers and get onto the host only to feed. This condition is known to exist in other closely related genera and species, and could account for the small numbers of mites found on the host animals in this study.

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A Report on Seasonal Food Habits and Life History Notes of the Florida Duck in the Vicinity of Lake Okeechobee, Glades County, Florida

Stephen L. Beckwith and H. Jay Hosford
University of Florida, Gainesville

To sportsmen of southern Florida an important component of waterfowl hunters' bags is the bird known as the Florida duck (*Anas f. fulvigula* Ridgway). This nonmigratory species occurs in peninsular Florida from the latitude of Gainesville (Alachua Co.) southward, reaching its greatest abundance in the vicinity of Lake Okeechobee. Its value as a game bird is indicated by the fact that, in areas where it occurs, it comprises about 10 per cent of the total waterfowl kill (Chamberlain, 1950). Such a kill has been variously estimated to comprise from 40 to 60 percent of its total pre-hunting season population (Chamberlain, 1951a; Jennings, 1953), but in spite of such excessive hunting pressure Florida duck populations are remaining steady or even slightly increasing in numbers (Chamberlain, 1951b; Jennings, 1952).

The following study was initiated as part of Florida Federal Aid Project W-19-R in 1953 by H. Jay Hosford, a graduate assistant at the School of Forestry, University of Florida, for his thesis subject. Its objectives were to study the food habits of the Florida duck as well as to gather information on nesting activities, brood survival, sequence of molts, and other pertinent facts relative to the life history of this game bird. Unfortunately, however, Mr. Hosford's death occurred before he could complete his work or summarize the results of his study. Since the senior author served as chairman of Mr. Hosford's graduate supervisory committee, he undertook to complete the analyses of the duck gizzards for the food habits phase of this investigation, and to summarize what had been learned during Hosford's study.

DESCRIPTION OF THE STUDY AREA

This study took place on a 22,400-acre tract bordering the northwest corner of Lake Okeechobee and located in Glades County, Florida, approximately 12 miles southwest of Okeechobee City. The topography over most of the area is relatively level, but in a few places, near the edge of the Lake, there are

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very slight undulations in the terrain. Elevations range from 22 feet above sea level in the vicinity of Moore Haven, in the southwest corner of the Lake, to 34 feet above sea level at Okeechobee City. Cattle raising and truck cropping (largely tomatoes, but some watermelons) are the principal forms of land use.

Surface water is normally abundant and well distributed throughout the study area. Much of it occurs in numerous shallow ponds that vary in size according to the amount of rainfall. Additional open water occurs in drainage ditches that criss-cross the area in an effort to remove excess water so that the land can be farmed. Artesian wells scattered over the area augment the supply of water in the ditches. There are approximately 91.6 miles of old ditches and 7.5 miles of new ditches in the study area. Although these ditches usually contain water, while the ponds may occasionally become dry, both form an important feature of the Florida duck habitat.

Climatic data for Moore Haven, about 20 miles southwest of the study area, are presented in fig. 1. In general the climate is characterized by moderately cool, dry winters, and warm, wet summers. The average annual
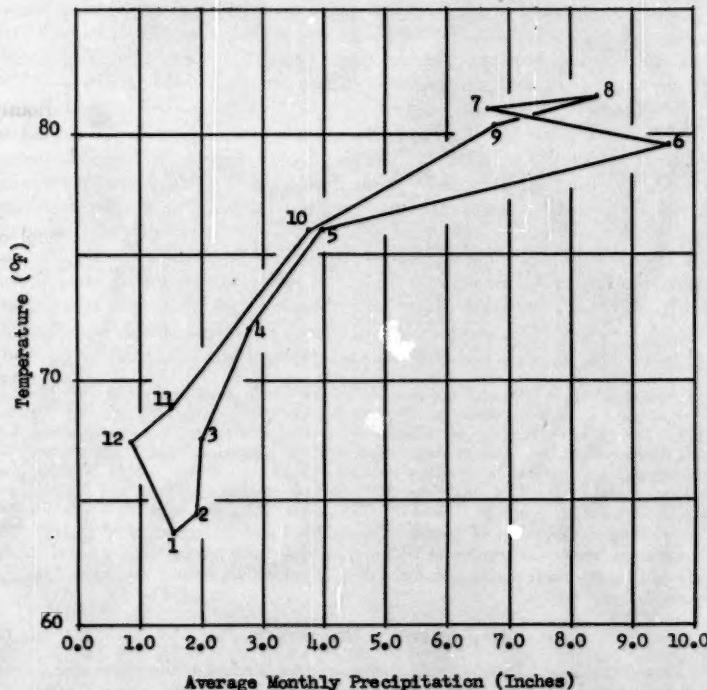
Fig. 1.—Climatograph for Moore Haven, Glades County, Florida. Data average for a 36-year period.

temperature is 73.2° F, and the average annual precipitation is 49.95 inches. Average monthly temperatures range from 64.0° F in January to 81.4° F in August. Temperature extremes during the period of this investigation ranged from a maximum of 98° F on May 28, 1953 to a minimum of 36° F on December 16, 1953 (U.S. Department of Commerce, 1954 and 1955).

Hurricanes periodically sweep across or near the study area, but there was only one such storm of any consequence during the period of this investigation. This storm was slightly below hurricane intensity and occurred in October 1953, travelling toward the northeast directly across the area of study. There is no indication that hurricanes are a menace to Florida ducks although they are known to do considerable damage to bobwhite (*Colinus virginianus*) and other types of ground-dwelling bird life (Frye, 1954).

The vegetation of the area was studied in an extensive manner by the use of aerial photographs at a scale of approximately 8 inches = 1 mile. These photographs were examined in the office under a dot-grid sheet having 36 dots per 10 acres. A tally was made of all the dots occurring in each type of vegetation, and the total number of dots was determined. The number of dots in each type was then expressed as a percentage of the total number of dots to arrive at an estimate of the percentage of the area covered

TABLE 1.—Types of vegetation occurring on the Florida duck study area expressed as percentages of the total area occupied by each type.

Type of Vegetation	Percent
1. Wet prairies, seasonal marshes and grassy sloughs	64.4
2. Ponds	
a. Approximately 50 percent *Pontederia* spp.[1] and *Sagittaria* spp. and 50 percent *Persicaria* spp.	6.1
b. Mixture of *Pontederia* spp. and *Sagittaria* spp.	4.6
c. Predominantly *Scirpus* spp.	1.5
d. Grassy	0.6
e. Predominantly *Persicaria* spp.	0.1
Total ponds	12.9
3. Old fields (principally tomato fields)	9.8
4. Southern waxmyrtle (*Cerothamnus ceriferus*)	7.9
5. Tomato fields	1.7
6. Cabbage palmetto (*Sabal palmetto*)	1.6
7. Jamaica sawgrass (*Mariscus jamaicensis*) marsh	1.3
8. Other herbaceous perennials	0.3
9. Miscellaneous, including pondcypress (*Taxodium ascendens*), spoil banks, etc.	0.1
Total	100.0

[1] Scientific names of grasses are drawn from Hitchcock (1935). All other plant scientific names are in accord with Small (1933). Common names are drawn from Standardized Plant Names (1942).

by each kind of vegetation. On this basis the vegetation on the study area is approximately as given in table 1.

TECHNIQUES OF STUDY

Many of the life history data presented were obtained by making periodic visits to the study area and recording the numbers and behavior of the birds observed. In addition, beginning with October 1953, an attempt was made to collect at least six specimens monthly. These were used primarily for determining food habits, but weights and measurements, as well as notes regarding coloration, sexual development, and other conditions were also taken. Additional gizzards for food habits analyses were obtained by contacting hunters at a fish camp five miles northeast of the study area. It is assumed that the gizzards so obtained represented a valid sample of the food habits of birds in the vicinity of the study area. The number of birds collected and the additional number of gizzards analyzed are listed by months in table 2, which shows that no birds or gizzards were obtained for study purposes during December 1953 and also during September and October 1954.

The food habits phase of this investigation was based upon the analysis of a total of 144 gizzard contents (table 2). All gizzards collected through July 1954, exactly one-half of the total number, were analyzed by Mr. Hosford, whereas the analysis of the remaining gizzards was accomplished by the senior author with the assistance of student labor. Individual food items were measured volumetrically by the water displacement method, and final results were expressed as percentages of the aggregate volume comprised by each item.

The growth rate of young Florida ducks in confinement was determined

TABLE 2.—Number of Florida ducks and additional gizzards obtained for study purposes by months.

Month	Birds collected and measured	Additional gizzards	Total gizzards
October 1953	7	0	7
November 1953	11	13	24
December 1953	0	0	0
January 1954	2	0	2
February 1954	6	0	6
March 1954	6	1	7
April 1954	6	0	6
May 1954	8	0	8
June 1954	6	0	6
July 1954	6	0	6
August 1954	6	0	6
September 1954	0	0	0
October 1954	0	0	0
November 1954	0	66	66
Totals	64	80	144

by making periodic measurements on an entire brood of seven ducklings that was captured on the day the birds hatched, May 3, 1953. These ducklings were kept under observation until they reached the age of four weeks, at which time they were transferred to a larger pen at Gist's Bird Farm, McIntosh, Florida, and measurements on them proved impracticable because of the amount of travel involved.

In the discussion that follows, the period included in this investigation has been separated into seasons which consist of the following months: Spring —February, March and April; Summer—May, June and July; Fall—August, September, and October; and Winter—November, December, and January. Although the seasons in southern Florida are rather indistinct by northern standards, there is still sufficient variation from one season to another to have an important influence upon all biological activity.

RESULTS AND DISCUSSION

PHYSICAL CHARACTERISTICS OF THE FLORIDA DUCK

Weight and size.—Florida ducks are moderately large in regard to both weight and size. The average adult male, based upon thirty birds, weighed 1030.3±107.2 grams (maximum 1280.1), whereas eleven adult females averaged 968.0±76.0 grams (maximum 1131.8).

The average length of the forty-one adult birds was 573±30.0 millimeters and the average wing spread was 849±44.1 millimeters.

Color differences between the sexes.—The most prominent means of determining sex in Florida ducks on the basis of color is by an examination of the bill. In males the bill is a solid color, tending to be a brilliant yellow. In contrast, however, the bill of females is likely to be somewhat darker, running toward a dull orange or a dark, dull yellow, and blotched with dark olive markings. These differences are such that bill coloring alone can be used for sex determination in the field. Another means of distinguishing between the sexes on the basis of color is by the appearance of the breasts. On males the breast is generally darker, and has a pronounced mottled or spotted effect, whereas on females the breast tends to be lighter, and the mottling occurs in more or less vertical lines. However, since there is considerable variation in breast coloration, this character cannot be relied upon entirely for separating the sexes.

LIFE HISTORY OF THE FLORIDA DUCK

Number of birds observed.—Repeated observations of Florida ducks, as recorded in Mr. Hosford's field notes, indicate that the birds occur in groups as large as thirteen in number, perhaps even larger, until the latter part of February. Beginning in March and continuing through July, which includes the breeding season, birds occur as singles (usually males), pairs, or quite frequently as triples (two drakes and one hen). Flocks as large as fifty in number and consisting principally of young birds occur during August. By the beginning of the hunting season in November the birds continue to occur in flocks of from six to twenty in number.

The opinion was held by Mr. Hosford that the combination of two drakes and a single hen mentioned above was an example of a "novice" drake (Hochbaum, 1944) attached to an active pair of birds. Hochbaum observed such surplus drakes with pairs of lesser scaups (*Aythya affinis*), redheads (*Aythya americana*), shovellers (*Spatula clypeata*), blue-winged teal (*Anas discors*), pintails (*Anas acuta*) and mallards (*Anas platyrhynchos*), and noted that extra males were more frequently observed in those species which showed the largest excess of males in the spring flight.

Mating.—The earliest record of mating, on the basis of field observations, is between the dates of February 7 and 17, 1954, when mating was known to occur in at least one pair during that period. However, judging from the grouping of the birds observed, the majority of the mating takes place during March.

Courtship.—Only one instance of courtship (probably of the post-nuptial type) was recorded during this study. This occurred on April 13, 1954. It consisted of the drake quacking persistently and bobbing its head up and down two or three times, sometimes even putting its head entirely under water. This process was repeated a number of times. The drake approached the hen by flapping its wings and bounding forward, and when copulation was attempted, the female made an attempt to escape but did not fly away.

Nesting.—Since only five nests containing eggs were found during this investigation, it is impossible to draw any definite conclusions about the nesting activities of the Florida duck. However, by using what few data were available, the nesting season was determined to extend from April through June, with the primary season being the month of April and the first week in May. This conclusion is based upon the nest data, the observation of a newly hatched brood on May 3, 1953 and two broods of ducklings both less than a week old on May 11, 1954, and the earliest date (July 21, 1954) that a young bird of the year was collected. It is in agreement with Bent (1923), and also is substantiated by the work of Singleton (1953), who regards April as the principal nesting month for the mottled duck (*Anas fulvigula maculosa*). The extension of the nesting season through June is indicated by the collection of hens still in the laying process as late as June 28, 1954.

Nests are circular in outline, measuring about 10½ inches across and from 1½ to 3½ inches deep. They are more or less lined with down, grass, or twigs. A common, although not necessarily preferred, nesting site is in tomato fields where three of the five nests examined were found. One nest occurred out in the open in an old watermelon field. The location of the fifth nest was not recorded.

Although the location of Florida duck nests is not dependent upon proximity to water, they are usually within easy reach of it. For example, in tomato fields the nests are placed on the hills of the planted rows. Water is usually available either between the rows themselves or in the larger drainage ditches at the ends of the rows.

Eight was both the largest and the most common number of eggs observed

per nest, in fact four out of the five nests contained this number of eggs. The fifth nest contained five eggs. Out of a total of sixteen eggs from which data are available, fifteen (94 percent) hatched. The remaining twenty-one eggs in the other three nests were destroyed by laborers, who removed all thirteen eggs from two nests, and by an undetermined predator that devoured the eight eggs in the third nest.

Brood growth.—One entire brood of seven ducklings was captured the day the birds hatched (May 3, 1953) and confined in a pen to observe their growth rate. The birds were started on a diet consisting of chopped boiled eggs and gradually switched to baby chick mash. Later they were fed a combination of the mash and duckweed. The growth of the young birds is presented in table 3.

Post-nesting season.—Following the nesting season the adult birds evidently go through a normal post-nuptial molt and become flightless for a period of a few days. Although this molting process was never actually witnessed, there is strong circumstantial evidence to point toward it. For example, no adult birds were observed, and none was collected, during the latter part of July and the first half of August. Furthermore, the three surviving birds of the brood mentioned above followed the normal molting sequence for ducks and became flightless during the month of July 1954. Additional evidence is the fact that mottled ducks in Texas were observed by Singleton (1953) to undergo the post-nuptial molt within the months of June and July.

Age determination.—Young Florida ducks possess the usual characters that are associated with their age, namely, a bursa of Fabricius, and an un-sheathed penis or an occluded oviduct (Hochbaum, 1942). The bursa of Fabricius appears first as a pouch that may be as deep as 42 millimeters in young birds during late July and early August. It persists until mid-February in some birds, appearing by that time as only a small indentation in the wall of the cloaca.

The structure of the penis ceases to be of value as an age determinant

TABLE 3.—The growth of young Florida ducks indicated
by their weights at known ages.

Duckling No.	Weight (grams) at age			
	1 day	9 days	16 days	27 days
1	28.6	58.2	122.0	247.1
2	31.4	75.6	150.6	244.3
3	29.1	68.4	120.6	222.2
4	31.9	84.1	163.4	189.9
5	30.8	79.1	165.4	235.2
6	32.6	78.4	162.3	271.7
7	31.9	86.0	166.2	240.8
Average	30.9	75.7	150.1	235.9

when it transforms from a small, unsheathed appendage to the large, sheathed organ that characterizes adults. In Florida ducks, on the basis of field observations, this transformation frequently occurs between the second week in August and the latter part of October. Hochbaum (*op.cit.*), working in Canada, states that in mallards this change occurs as early as late October in young birds only five months old. Applying this age to the known nesting season of Florida ducks, it can be assumed that in some individuals of this species the transition from the immature to the adult penis occurs during the month of September. Consequently, the bursa of Fabricius, and not the condition of the penis, should be used to indicate the age of young drake Florida ducks after this time.

The present investigation yielded no new information regarding the condition of the oviduct as a criterion for age in young female Florida ducks. However, judging from the work of Hochbaum (*op.cit.*), it is logical to assume that the oviduct remains occluded until just before the beginning of the breeding season in February.

FOOD HABITS OF THE FLORIDA DUCK

Within the fifteen-month period of this investigation the food of Florida ducks, on the basis of the identified items only and exclusive of the grit content, consisted of 87.2 percent vegetable matter and 12.8 percent animal matter. This proportion varied from almost 100 percent vegetable matter and only a trace of animal matter during the fall and winter seasons to 61.3 percent plant material and 38.7 percent animal matter in the summer (table 4). Variations in the utilization of plant and animal foods comprising 1.0 percent or more of the total gizzard contents during any one season are presented graphically in fig. 2. Other plant and animal foods consumed in significant amounts by Florida ducks are presented in table 5. Food items of only very minor importance to Florida ducks have been omitted from the lists included in this report.

Plant foods.—Florida ducks utilized a total of 77 species of plants which were included in 51 genera. Marked variations occurred in the consumption of

TABLE 4.—Percentages of plant and animal matter consumed by Florida ducks according to season on the basis of identified material only.

Season	Plant Matter	Animal Matter
Fall 1953	100.0	Tr[x]
Winter 1953-54	100.0	Tr
Spring 1954	81.7	18.3
Summer 1954	61.3	38.7
Fall 1954	100.0	Tr
Winter 1954-55	92.0	8.0
Average	87.2[y]	12.8

[x] Tr = less than 0.1 per cent.
[y] Average figures based upon aggregate volumes rather than upon percentages above.

Food Item	Fall 1953 (7)[x]	Winter 1953-54 (20)	Spring 1954 (19)	Summer 1954 (20)	Fall 1954 (6)	Winter 1954-55 (66)
PLANT						
Axonopus furcatus (Big carpetgrass)						
Paspalum ciliatifolium? (Fringeleaf paspalum)						
" dissectum (Mudbank paspalum)						
Panicum agrostoides? (Redtop panicum)						
" bartowense (Bartow panicum)						
Echinochloa walteri (Coast cockspur)						
Setaria geniculata (Knotroot bristlegrass)						
Cyperus odoratus? (Flatsedge)						
Eleocharis cellulosa (Gulfcoast spikesedge)						
" equisetoides (Jointed spikesedge)						
Scirpus robustus (Saltmarsh bulrush)						
Rynchospora corniculata? (Horned beakrush)						
Cerothamnus ceriferus (Southern waxmyrtle)						
Persicaria portoricensis (Puerto Rico smartweed)						
" punctata (Dotted smartweed)						
Cabomba caroliniana (Carolina fanwort)						
Psidium guajava (Guava)						
Centella repanda						
Jacquemontia sp. (Vine)						
Lycopersicon lycopersicon (Tomato)						
Ambrosia elatior (Ragweed)						
ANIMAL						
Gastropoda (Snail shells)						
Coleoptera: Dytiscidae (Water beetles)						
Haliplidae (Water beetles)						
Hydraenidae? (Water beetles)						
Hydrophilidae (Water beetles)						

Fig. 2.—Plant and animal foods of the Florida duck comprising 1.0 percent or more of the total gizzard contents in any one season. The width of the line is proportional to the relative importance of each item.

x Figures in parentheses refer to the number of gizzards included.

these plant foods from one year to the next as well as from season to season. For example, the food habits of birds representing the fall 1953 were quite different from those of birds collected during the fall 1954. Accordingly, during the fall of 1953 the most important foods, listed in the order of relative use, were ragweed (*Ambrosia elatior*), fringeleaf paspalum (*Paspalum ciliatifolium?*[2]), knotroot bristlegrass (*Setaria geniculata*), *Jacquemontia* sp., and dotted smartweed (*Persicaria punctata*). In contrast, the principal foods during the fall of 1954 were redtop panicum (*Panicum agrostoides?*), dotted smartweed, big carpetgrass (*Axonopus furcatus*), *Centella repanda*, fringeleaf paspalum, and mudbank paspalum (*Paspalum dissectum*).

Some of the differences mentioned above can be attributed to the fact that the 1953 gizzards were collected only during October, whereas the 1954 gizzards represent only the month of August. However, the absence of ragweed, in particular, from the 1954 specimens and variations in the amounts of the different plant species consumed suggest actual differences in Florida duck food habits during the two fall seasons.

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[2] A question mark following a scientific name indicated that seed characteristics were not distinctive enough to permit exact specific identification. Such cases occurred principally among the grasses and the sedges.

Marked variations also occurred in both the kinds of plants and the amounts of the same species utilized during the two winter seasons, as determined by gizzards collected almost exclusively during November of each year. For example, jointed spikesedge (*Eleocharis equisetoides*), horned beakrush (*Rynchospora corniculata?*) and saltmarsh bulrush (*Scirpus robustus*) were all consumed in relatively large amounts by Florida ducks during the winter 1954-55. These three species, however, were absent entirely from gizzards of birds collected during the previous winter. Variations in the consumption of the same foods during the two winter seasons are apparent in the data for Gulfcoast spikesedge (*Eleocharis cellulosa*), Carolina fanwort (*Cabomba caroliniana*), Puerto Rico smartweed (*Persicaria portoricensis*), and ragweed.

' Spring foods of the Florida duck, as indicated in figure 2, include dotted smartweed, Puerto Rico smartweed, coast cockspur (*Echinochloa walteri*), knotroot bristlegrass, and southern waxmyrtle. Summer foods include Bartow panicum (*Panicum bartowense*) as by far the most important food item, as well as dotted smartweed, Puerto Rico smartweed, mudband paspalum, *Centella repanda*, and tomato (*Lycopersicon lycopersicon*).

Variations in the food habits of Florida ducks from year to year can be logically explained by differences in the availability of the various foods to the birds. Of particular importance in altering availability are the changes in water depths. The previously mentioned differences between the 1953-54 and 1954-55 seasons illustrate the effect of water depths upon the food habits of Florida ducks. Precipitation data for stations located about Lake Okeechobee all indicate that the months of August, September, and October, 1953 had above normal amounts of rainfall, part of which fell during the passage of a tropical storm of nearly hurricane intensity across the northwest portion of Lake Okeechobee during October of that year. As a result of such large amounts of precipitation, much of the land was flooded, enabling ducks to feed over extensive areas of pasture and cultivated lands that were normally not available to them. Florida duck food habits during the fall 1953 and the winter 1953-54 reflect these conditions, since such species as ragweed, fringeleaf paspalum, and knotroot bristlegrass, which occur in such locations, are all relatively important (fig. 2).

Water levels were entirely different in 1954. During this year deficient amounts of rainfall were recorded through the fall and early winter periods, and surface water during the latter half of 1954 was confined largely to normal ponds, drainage ditches, or to Lake Okeechobee itself. Consequently, the feeding activities of Florida ducks were restricted to such areas. During the winter of 1954-55, fig. 2 indicates that the birds fed principally upon either emergent marsh plants, such as spikesedges, beakrushes, bulrushes, and smartweeds, or upon aquatic plants such as Carolina fanwort. The importance of guava (*Psidium guajava*) at this time can be logically explained by the occurrence of this species along the banks of drainage ditches.

Animal foods.—It was mentioned previously that spring and summer, 1954, were the periods of heaviest use of animal matter by Florida ducks. During these two periods animal material comprised 18.3 and 38.7 percent, respectively, of the total identified material (table 4), or 10.6 and 25.0 per-

TABLE 5.—Additional plant and animal foods consumed by Florida ducks with the period of use as indicated.

FOOD ITEM	Fall 1953	Winter 1953-54	Spring 1954	Summer 1954	Fall 1954	Winter 1954-55
PLANT MATERIAL						
Cyperus compressus (Flatsedge)	x	x	x		x	
Scirpus spp. (Bulrush)			x	x	x	x
Rhynchospora spp. (Beakrush)	x	x	x	x	x	
Mariscus jamaicensis (Jamaica sawgrass)		x	x	x		x
Pontederia sp. (Pickerel weed)		x	x	x		x
Brasenia shreberi (Watershield)		x	x			x
Proserpinaca sp. (Mermaid weed)		x	x	x		x
Pitilimnium capillaceum (Mock bishopweed)	x	x	x	x	x	x
Phyla sp. (Frog-fruit)	x	x	x	x	x	x
ANIMAL MATERIAL						
Pelecypoda (Mussels)		x		x		
Decapoda (Freshwater shrimp)				x		x
Hemiptera (Bugs)						
Belostomatidae (Water bug)				x		x
Nepidae (Water scorpion)				x		x

cent, respectively, of the total gizzard contents (exclusive of the grit content).

The most important forms of animal matter were various kinds of water beetles of the families Hydraenidae (?), Hydrophilidae, Dytiscidae, and Haliplidae (fig. 2). Snail shells were another important component of Florida duck gizzards, especially during the winter of 1954-55. It is unknown whether these were taken intentionally for the protein content of the animal bodies or for the calcium and other minerals contained in the shells, or whether they were taken accidentally as grit or mistaken for seeds. Regardless of why snail shells are utilized by Florida ducks, it is logical to assume that they furnished the birds with minerals and other substances that are vital to their continued well-being.

The high utilization of snails during the winter season of 1954-55 also can be correlated with the low water levels that occurred at that time. Under such conditions the birds were restricted to areas where the snails normally occurred, and, because of the shallow water, they were able to feed on the snails if they so desired. High water levels could likewise explain the absence of snails from the duck gizzards collected during the 1953-54 winter season.

Lead shot.—A total of fourteen (9.7 percent) of the 144 gizzard contents contained lead shot. In at least eight of the gizzards (5.5 percent of the total) the shot showed evidences of wear, indicating that it had been mistakenly ingested by the birds as food material. In the remaining six gizzards the appearance of the shot was such that it was impossible to determine if the shot had been ingested as food or shot into the gizzard when the bird was killed.

SUMMARY

This investigation was undertaken primarily to become familiar with the food habits of the Florida duck and secondarily to obtain information regarding the life history of this bird.

The study took place on a 22,400-acre area of more or less level land covered predominantly by wet prairies, seasonal marshes, grassy sloughs, and a variety of mostly shallow ponds.

Moderately cool, dry winters, and warm, wet summers characterize the climate of the study area.

Pairing off in the Florida duck commences as early as February and is completed during March.

The nesting season extends from April through June, with the principal activity being in April and the first week of May. Nests commonly contain eight eggs, and are frequently placed in tomato fields.

Circumstantial evidence indicates that wild adult Florida ducks undergo the normal post-nuptial molt during the months of July and August.

Age in young Florida ducks is reliably indicated by the bursa of Fabricius, in both sexes, and the occlusion of the oviduct in females alone. The structure of the penis becomes valueless as an age determinant when it assumes the characteristics of an adult during the month of September.

On the basis of identifiied material only, Florida ducks consumed an average of 87.2 percent plant material and 12.8 percent animal matter during the fifteen months included in this investigation.

The consumption of plant foods varied according to their availability as determined by the season of the year and both the extent and depth of surface water. The amount and distribution of rainfall are important in this latter respect.

Animal matter was consumed principally during spring and summer periods.

Ingested lead shot occurred in a minimum of 5.5 percent of the gizzards examined.

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Nesting Habits of the Yellow-billed Cuckoo

Norman A. Preble
Northeastern University, Boston, Massachusetts

The following observations on the nesting and related habits of the Yellow-billed Cuckoo (*Coccyzus americanus americanus*) were made during July, 1941, on Gibraltar Island, Put-In-Bay, Ottawa County, Ohio. This island is approximately 4½ miles from the mainland. The nest, when found on the afternoon of July 5, contained two eggs. It was situated about 8 feet above the ground, in a red cedar (*Juniperus virginiana*) and rested rather insecurely in the fork of a horizontal branch, 10 inches from the main trunk. The tree was located 20 feet from the edge of a cliff which forms much of the northern boundary of the 6-acre island. Thick branches on the northwest side of the tree served to protect the frail nest from heavy winds which, upon two occasions, swept forcefully across the lake. The exterior depth of the nest was two inches and the cup was lined with a few leaves and fine tendrils and measured approximately 4 inches in diameter and 1¾ inches at the point of its greatest depth. The young, when removed for weighing, would grasp twigs firmly with their feet, with the result that an accurate weight of this nest could not be obtained.

The first observations and notes were made from a canvas blind erected in an open space some 20 feet from the nest, at 7:30 P.M. on July 5. A 7X field glass was used. Between this date and July 21 inclusive, a total of 51 hours was spent in observation of the nest. These daily periods of study varied from one hour to 16 hours. Incubation of the 2 eggs continued for 5 days more and at 8:45 A.M. on July 10, the first young was discovered emerging from the shell. Twenty-three hours later, on July 11 at 8:00 A.M. the second young had completely extricated itself from the shell.

INCUBATION

A Yellow-billed Cuckoo, carried twigs in its bill in the vicinity of the study nest on July 2. As the nest itself was not discovered until July 5 many data of interest and value relating to the nest-building and incubation phases of activity were lost. On July 5, the blind was erected and the nest was observed from 7:30 P.M. to 9:00 P.M. The adult remained incubating the 2 eggs present all during this period. The following morning the bird was observed from 5:30 A.M. until 6:30 A.M. During the first few minutes a cuckoo called faintly in the distance, and the incubating bird left immediately to remain away for an interval of 10 minutes. On its return, the approach to the nest was made very cautiously. It settled on the eggs which were shifted twice during one 3-minute interval, by means of the bill. It could not be observed whether the feet were employed in this act or not. The

shifting of eggs occurred sometimes at regular 10-minute intervals and was accompanied by a change in the bird's position. The new position was maintained for one minute to 35 minutes. A considerable amount of calling by birds in the distance was heard during the incubation period which resulted invariably in attracting the adult and the nest left unattended. The longest period of absence was an hour and one-half during which, again, much calling by Yellow-billed Cuckoos was noted. Also during this phase of the nesting cycle, the adult paid a great deal of attention to the blind; notably so, whenever the binoculars were moved. It was not determined at this time whether one or two adults participated in incubation for it was not recognized until later that the distinctive mandible coloration could be used to establish the identity of the attending adult. However, no exchanges were noted to have occurred between the parents during this time.

There were approximately 24 hours difference between the hatching times of the two eggs and on July 10 the nest contained one nestling and one egg. On seeing the young (A) for the first time, the adult uttered a rapid *cuk-cuk-cuk* note which had not been heard before and it was also given on later occasions when motion within the blind seemed to stimulate the adult and also was given when an attempt was made to live trap the bird for banding. The nest was observed for 2 hours in the morning of July 10 while the parent was absent from the nest on three occasions for 10 to 35 minutes. At 4 o'clock in the afternoon of the same day, a heavy thunderstorm struck the island with attendant heavy rain and wind. The adult returned promptly and faced into the wind with the back depressed to about the level of the nest, waited out the storm, and continued to brood when observations were ceased at dark.

NESTLING STAGE

The initial reactions of a newly-hatched Black-billed Cuckoo (*Coccyzus erythropthalmus*) have been well described by Herrick (1910) and Spencer (1943) and these accounts do not differ appreciably from those observed for the Yellow-billed Cuckoo in the present study. Yet, certain of the early behavior characteristics of these two young may be of interest.

At 8:45 A.M. on July 10 the adult was flushed from the nest and the first of the young (A) was seen just emerging from the egg. The shell had been pipped around its lesser circumference and hatching had progressed to a point where the two halves of the shell were only partly covering the body. The head was tucked beneath the abdomen, and by several forceful rhythmic kicks with the feet, the chick eventually extricated itself from the shell, straightened out the neck and lay quiet. This phase of hatching lasted 4 minutes. The inner surface of the egg was moist, but the young bird was perfectly dry. Both Herrick (1910) and Spencer (1943) in describing the appearance of newly-hatched Black-billed Cuckoos mention the fact that in this species, too, the egg membranes were damp, though the young were dry.

Young A was first fed by the parent one hour after hatching. The following morning July 11, at 7:00 A.M., the nest was visited again and the adult found on it. The bird was not disturbed at this time and on return to

the nest, an hour later, the second young (B) had hatched. The time of the first feeding of young B was not determined.

The general appearance of the newly-hatched young shows the exposed skin areas to be blackish in color and rubbery in general appearance; tarsi and feet light slate blue; mandibles similarly colored, the upper one tipped with white and the lower one tipped with black; minute temporary down sheaths were well distributed over the body, marking the locations where these are later to be replaced by the finely striated, lead-colored feather shafts; flanges whitish, delicately tinged with pink, inner surfaces of the mouth cavity reddish; apical portion of the tongue marked at the base by a medially located white disc. Herrick (1910) in his figure of the target pattern of a newly hatched Black-billed Cuckoo indicates a definite tri-lobed pattern in the two largest pads located lateral and posterior to the tongue pads. This pair of pads in the Yellow-billed Cuckoo measured approximately 8 mm in length and 1 mm in width and bore several posteriorly directed spines. As the nestlings mature these spines increase in number and the pads proportionately larger. However, instead of having a lobed pattern as in the Black-billed Cuckoo, these were lenticular in shape and lacked the lobations. Two other recently hatched young, examined later, revealed the same pattern.

An approach to the nest was made in order to observe the hatching process described above. About 10 minutes after this had been completed, fingers placed at the edge of the nest probably jarred it slightly whereupon the nestlings immediately responded with a begging reaction and a faint hissing *qua-a-a-a* series of notes. Herrick (1910) mentions nest-jarring as a stimulus for the begging response during the early period of nest life. The adult did not return until a half-hour after the young had hatched. It approached the nest carrying a mayfly and uttered a very faint but rapid *cuk-cuk-cuk*. The mayfly was then eaten by the adult after which it slowly approached the nest, ruffled up the feathers and settled on the nest. The adult regarded the nest contents with a cocked head after which she seemed to ignore the young one and continued to incubate the remaining egg for 20 minutes. At the end of this period the adult left to return 8 minutes later with a small fly. At this second visit to the nest, the food was offered to the young. The bill was inserted into the throat and held there nearly a minute before the insect was swallowed. Following this first feeding the adult settled on the nest without attempting to remove any of the fragments of egg shell. The bird remained on the nest for 12 minutes and then left. After an absence of 10 minutes, it returned for a third time carrying a caterpillar. After feeding the young, the adult usually left the nest by the same route throughout the nesting period. On approaches to the nest various routes were used. The young was promptly offered the food but was very slow about swallowing it. The parent then proceeded to crush a few pieces of egg shell in the bill. Some was swallowed but on checking the nest later it was found that the greater bulk of the shell remained in the nest. The reactions of the young to these early visits of the parent could not be directly observed because of their small size and the angle of vision at the time. One and one-half hours after hatching the nestling was able to raise its head well above the rim of the nest while being fed. At this time too, a male red-winged blackbird

fed in the cedar tree not over 2 feet from the nest. The adult cuckoo looked in its direction but did not attempt to drive it away.

The begging reaction of the young consisted of stretching the neck, elevating the head to a vertical position and opening the mouth to its full capacity. These movements were accompanied vocally and also by a fluttering of the wings which became progressively more rapid as the young advanced in age. On the first and second days of nest life the wing beats were at a rate of 2 per second, and were continued until they were fed. On the third day a *quck* note was added to the begging complex which was continued throughout the remainder of their nest life. No clue to its significance if any, was ascertained. While observing these young, all begging reactions were recorded irrespective of whether the adult was at the nest or not. On July 13, when young A and B were 3 days and 2 days old respectively, the adult returned to the nest and stopped momentarily 2 feet from the nest. Both young remained quiet. It then moved to within a foot of the nest where it remained 30 seconds and still no begging response was given by the young. Both young finally begged, but not until the adult actually stepped into the nest itself. The begging reaction was also initiated a few minutes after hatching by touching the nest and was always performed when the adult returned with food.

The eyes of the older nestling (A) did not open simultaneously for when these were examined on the third day (80 hours) the right eye was about half open while the left eye remained completely sealed. Two and one-half hours later the left eye began to open. At 5 days (120 hours) the nestling appeared quite aware of its surroundings. On the sixth day (151 hours) both eyes were well-opened, with the lids only slightly narrowed.

On July 19 it was possible to conduct only brief observations of the young which were 8 and 9 days old. At 4:00 P.M., young A (223 hours) weighed 40.7 grams. Most of the feather shafts had broken with the exception of those just above the bill. The feather shafts of young B were not ruptured as extensively as in A. Shortly after 4:00 P.M., young A left the nest for the first time by hopping to a nearby branch and disappeared in the foliage. The nest was checked again at 10:30 P.M. to find that young A had returned to the nest. The following morning, July 20, at 8:45 the nest contained young B only. Before noon of that day, B had left. Again at 4:00 P.M., the vicinity of the nest was examined to find young B perched on a branch immediately below the nest, and made no effort to escape. Its weight at this time was 37.7 g. It was then released and not observed again. Both young A and B were banded July 17, 1941 with Biological Survey Bands Nos. B-320596 and B-320595, respectively. Both of the young on July 12 (A—age, 55 hours; B—age, 33 hours) were capable of sustaining their weight from a stick but the muscles fatigued after a few seconds and they relaxed their hold. They were unable to support their weight for any length of time until shortly before they left the nest permanently. In the case of young A it was first observed to support itself on its legs at 3 o'clock July 19 (222 hours) and at 4 o'clock, it left the nest. The young left the nest at the age of 9 days (220 hours).

PARENTAL CARE

The role of supplying food to the young fell, for the most part, to one parent. This individual was recognizable early in the study because of a very extensive wash of yellow on the upper mandible which extended to the level of the nostrils. On July 14 this bird was trapped and a Biological Survey Bird Band No. 320600 was placed on the right tarsus. A yellow celluloid band was added to the left tarsus for ease of identification. The following measurements were secured: wing, 146 mm; tail, (worn) 153 mm; tarsus, 26.9 mm; exposed culmen, 26.2 mm, the weight was 58.8 g. A conspicuous incubation patch was present suggestive but not conclusively establishing it as a female, as both males and females are known to incubate.

On July 16 the nest was under continuous observation from 5:00 A.M. to 8:00 P.M. During this 15-hour period, 39 visitations (table 1) to the nest were made of which 32 were with certainty made by the banded adult. Only once during this time was it positively ascertained that the young were fed by an unbanded bird. At 9:15 A.M., the young were fed by the banded adult. One minute later an unbanded bird fed the young and left immediately. The closeness of the feedings would perhaps have provided sufficient evidence too of both parents cooperating in this instance. The virtual absence of the other parent in caring for the nest may be explained by the presence

TABLE 1.—Nesting activity of the Yellow-billed Cuckoo

Date observed	July 13, 1941	July 16, 1941
Hours observed	(16 hours) 4:30 A.M. to 8:30 P.M.	(15 hours) 5:00 A.M. to 8:00 P.M.
Age of nestlings	Yng. A 67¾-83¾ hrs. (3rd day)	Yng. A 140-155 hrs. 6th day)
	Yng. B 45.5-61.5 hrs. (2nd day)	Yng. B 117½-132½ hrs. (5th day)
No. of nestlings	2	2
No. of adults nests visits and absences	20	39
Duration of absence	30 min. (1-86 min.)	18 min. (1-67 min.)
Total time absent	10 hours	12 hours
Sex of brooding bird	?	?
Times brooded	7	2
Total time brooded	3 hrs., 25 min.	2 hrs., 25 min.
Feedings	15	31
Visits without food	0	8
Average time lapse between feedings	64 min. (5-180 min.)	29 min. (1-139 min.)
Duration of feeding act	10-90 sec.	10-300 sec.
Number begging reactions	52 (Av. once every 20 min.)	9 (Av. once every 113 min.)
Duration of begging reactions	20 sec. (1-90 sec.)	4 sec. (1-10 sec.)
Nature of food	Caterpillars, 13	28
	Grasshoppers, 1	0
	Other Insects, 1	3
Nest sanitation	Excreta eaten, 5	6
	Excreta Removed, 2	6

of an earlier brood from the same pair, or by polygamy. Relative to the possible presence of an earlier brood, Dr. Walker observed two almost fully grown young birds on the island on July 13. On July 15 he saw a young bird being fed by an adult but was unable to determine whether the adult was banded or not. Later, additional evidence supporting the hypothesis of another brood, was added by the discovery of a recently used nest. On the basis of these data, it seems quite possible that one of the parents was attending the young of an earlier brood. Further observations made by Dr. Walker a year later, on Gibraltar Island, of a Yellow-billed Cuckoo's nest indicated that both male and female shared equally in brooding and caring for the young. Dr. Ned Dearborn (*in litteris*) informed me that he had known males to incubate the eggs and brood the young. He determined the sex by collecting the birds. He did not state, however, whether or not these were paired individuals.

The most significant observations concerning the degree of attentiveness and inattentiveness of the adult to the nestlings were obtained on July 13 and July 16, when the nest was under constant observation from dawn to dusk. These and related data are summarized in table 1. An analysis of these reveals that as the young advanced with age, nest visitations by the attending adult became more frequent; the lapse of time during absences from the nest became markedly less, decreasing from an average of 30 to 18 minutes. There was also an increase in total time absent from the nest. This might be accounted for because of increased demands occasioned by the presence of an earlier brood which it tended, but is definitely accounted for by the fact that the adult spent less time at the nest because the young were able to swallow food with greater facility on July 16 than before. The amount of brooding decreased markedly over 2 days and the two instances of brooding on July 16 were caused by rain. It was not established definitely that the adult brooded the young throughout the night, though in this regard it was noted that on July 10, when the nest contained one egg and one nestling only a few hours old, a thunderstorm occurred attended by heavy winds and rain. This began at 4 o'clock and the rain continued throughout the early evening. When the nest was visited at 7 o'clock the following morning, the wet and ruffled feathers of the adult were strongly suggestive in this instance, that brooding continued through the night.

As the young became more mature the begging reactions were less in evidence and of shorter duration. The length of time required by the young in feeding showed considerable variation because of the nature and size of food offered. Particular difficulty was noted on a few occasions when the parent delivered an exceptionally large caterpillar. The first observation of this occurred on July 13, when the adult returned with a large green caterpillar and offered it to one of the young which experienced difficulty in swallowing it. The adult repeatedly grasped and tugged at the free end finally pulling it loose from the young and ate it. The events lasted for 3 minutes. Three-quarters of an hour later the adult brought another similar-sized caterpillar and, again, there was trouble in swallowing but finally managed the situation perhaps aided by the adult not being so persistent in pecking at the mouth of the nestling.

Although it could not be established definitely that a previous brood from the same parents was present on the island, the probability was high. First, because of the fact that this nest was attended almost exclusively by one parent in a species where both usually share such responsibilities; secondly, by the observation of an adult cuckoo feeding young in the vicinity of the nest and thirdly, by finding a recently-used cuckoo's nest not far from the one which was studied.

The number of nest visits, when the parent was carrying food, increased over this 2-day period, (table 1). On July 13, fifteen visits were made with food, while on July 16, thirty-one such visits were made. On these dates, caterpillars were fed most frequently.

NEST SANITATION

The attending parent removed the fecal sacs (table 1). These were either carried away from the nest or else swallowed after the young had been fed and the two practices occurred with about equal frequency. The young were observed to defecate over the edge of the nest coincident with the times when their eyes were well-opened (sixth day). At this time too, the sacs

TABLE 2.—Weights of nestling Yellow-billed Cuckoos

		Young A					Young B		
Date	Age Days	Hrs.	Weight in grams	Remarks	Date	Age Days	Hrs.	Weight in grams	Remarks
Jul. 10	0	5¼	A.M.:		Jul. 11	0	1	A.M.: 8.5	
			P.M.: 9.8				9½	P.M.: 11.2	
Jul. 11	1	31¾	A.M.:		Jul. 12	1	25	A.M.: 12.4	
			P.M.: 14.2				33½	P.M.: 13.9	
Jul. 12	2	47	A.M.: 13.4		Jul. 13	2		A.M.:	
		55¾	P.M.: 16.4				58½	P.M.: 15.8	
Jul. 13	3		A.M.:		Jul. 14	3	73½	A.M.: 16.1	
		80¾	P.M.: 18.5				81½	P.M.: 22.1	
Jul. 14	4	95¾	A.M.: 20.2		Jul. 15	4	97½	A.M.: 21.5	
		103¾	P.M.: 25.1				109	P.M.: 28.7	
Jul. 15	5	119¾	A.M.: 24.0		Jul. 16	5	123	A.M.: 27.1	
		131¼	P.M.: 29.6				129	P.M.: 31.5	
Jul. 16	6	145¼	A.M.: 28.2		Jul. 17	6	145½	A.M.: 32.4	
		151¼	P.M.: 31.0				153½	P.M.: 40.6	
Jul. 17	7	167¼	A.M.: 29.0		Jul. 18	7	169½	A.M.: 32.4	
		175¾	P.M.: 39.0				177½	P.M.: 36.4	
Jul. 18	8	191¾	A.M.: 32.8	Entered climbing stage	Jul. 19	8	193½	A.M.: 30.7	Feather shafts erupted
		199¾	P.M.: 35.0				201	P.M.: 33.9	
Jul. 19	9	215¾	A.M.: 31.7	Left nest and returned	Jul. 20	9		A.M.:	
		223¼	P.M.: 40.7					P.M.:	
Jul. 20	10		A.M.:	Feather shafts erupted	Jul. 21	10		A.M.:	Entered climbing stage
			P.M.:				249	P.M.: 37.7	

were characterized by having very thin walls. At times the adult would remove them directly from the cloaca, for the young would usually expel these shortly after being fed, and in some instances they would be removed from the center or edge of the nest.

WEIGHTS OF THE YOUNG

Young A, five hours and 15 minutes after hatching weighed 9.8 grams; young B, one hour after hatching weighed 8.5 g. The latter weight, closer to the actual hatching weight, constituted approximately 14 percent of the weight of the adult which was 58.5 g when weighed on July 14. Daily weighings of the young birds were usually made at 8:30 A.M. and at 4:30 P.M. in order to obtain valid data for comparison. These weights are set forth in table 2. Both A and B gained an average of 4.9 g each day of nest life. Young A showed daily extremes of weight increment of 2.2 g to 10.0 g; young B, 1.5 g to 10.4 g. A normal weight-loss is expected to occur during the night, and the average losses sustained by the young at this time were: for young A, 2.3 g (0.8-6.0); for young B, 3.5 g (8.2-0.6). The total gains in weight in the nestling stage for A and B were approximately 30.9 g and 29.2 g respectively. A. C. Bent (1940) cites an observation made by Dr. Lawrence H. Walkinshaw who associated loss of weight in the young with the time of the rupturing of the feather shafts in the Yellow-billed Cuckoo. In the present study the feather shafts of both A and B were found ruptured on the eighth day (190 hours). Late afternoon weights of A and B on the seventh day were 39.0 and 36.4 g, respectively. Morning weights taken on the eighth day when the shafts had opened were 32.8 g for young A and 30.7 g for young B indicating a loss of 6.2 g for young A and 5.7 g for B. This loss was nearly twice the average loss sustained at night during the nestling stage.

MORTALITY OF NESTLINGS

Dr. Walker found an additional nest of the Yellow-billed Cuckoo in a small pear tree on South Bass Island on July 14, 1941. The nest contained two nestlings about ready to leave, another about 5 days old and a single egg. Weights taken of these young on July 15 were 33.6 g, 30.7 g, and 22.1 g, respectively.

On July 17 the two older birds had left though the youngest one was still in the nest. On July 19 the nestling was still alive and in the nest. On July 21 the young one was found dead, lying in the grass directly below the nest from which it may have fallen. It had grown considerably during the interval between visits, which led to the belief that it must have been fed to some extent, despite the presence of the two other young in the climbing stage. It is possible that the confusion caused by an attempt to capture one of the parents for banding, shortly before, may have contributed directly to the abandonment of the nest. Dr. Walker made further observations on another nest on Gibraltar Island during July 1942 which adds further light on nestling mortality. This particular nest contained three young. The youngest was estimated to be less than 24 hours old. It was notably smaller

than its companions which were known to be at least 2 days old, and seemed to be neglected at feeding time. It begged persistently after the others had been fed, which seemed to disturb the parents. Finally, one of the adults after pecking lightly at it picked it up and carried it away. Herrick (1910) states that in one or two cases which he observed, that the last young, if retarded in development, is sometimes left to starve.

SUMMARY

One nest of the Yellow-billed Cuckoo was observed between July 5 and July 21, 1941 for a total of 41 hours. Incubation of the eggs and care of the young were performed by a single adult. The possible presence of an earlier brood is suspect in modifying the behavior of the parents. The nest contained two eggs which hatched 24 hours apart. The newly-hatched young were dry and displayed a begging reaction immediately after hatching. One of the young was first fed one hour after hatching. Nestling Yellow-billed Cuckoos appear to differ from nestling Black-billed Cuckoos by the absence of lobes on the pair of pads lying lateral and posterior to the tongue. Full expansion of the eyelids does not occur until the fifth day. In one young, one eye opened $2\frac{1}{2}$ hours prior to the other. Dawn to dusk observations on the third and sixth days showed that as the young mature decreases were noted in the frequency and duration of the begging response, and in the amount of brooding, as well as the amount of time which the parent spent away from the nest; an increase in the number of absences and returns to the nest, feedings and in the total time spent away from the nest; the preferred food consisted of caterpillars, and excrement of the young was eaten or transported away from the nest with about equal frequency. A loss of weight is associated with the rupture of the feather sheaths on the 8th day. One young increased in weight from 8.5 g (one hour old) to 39.2 g, an increase of 361 percent. The young were first observed fully capable of supporting their weight only a few hours before leaving the nest. The nestlings left the nest in a flightless condition after spending 9 days (220 hours) in the nest.

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The Effects of Flooding on a Small Marsh in Central Connecticut

Kenneth H. Anderson
Department of Inland Fisheries & Game, Augusta, Maine

Jacob Shapiro
Wisconsin State College, Oshkosh

The Connecticut State Board of Fisheries and Game, as part of its wetlands program, purchased Charter Marsh in 1949. The area, comprised of 240 acres, was established as a refuge for waterfowl production and as a feeding and resting area during migrations. The study was commenced on February 1, 1952 and completed in June, 1953. The present report presents the data obtained on the mammal population during the study period. The authors gratefully acknowledge the assistance of James Bishop and Milton Arnold of the Game Management Division of the Connecticut State Board of Fisheries and Game.

The first records of Charter Marsh concern its value as a commercial cranberry bog. Cranberries were raised as early as 1861 and as late as the early 1900's. The bog was divided into an upper section to impound water and a lower section in which cranberries were grown. The dikes were constructed to provide adequate water that could be controlled by sluices to protect the cranberries from frost and insect depredation. The marsh, during recent years, was neglected. However, the local residents utilized it for blueberrying, cranberries, trapping, hunting and fishing.

The refuge is located in Tolland County, Connecticut, one and one-half miles west of the village of Tolland. It lies in a narrow valley bisected by the Skungamaug River. Oak and white pine are the dominant trees that surround the marsh. The stand was second growth, varying from 20 to 80 years of age, with an average of 40. The watershed is computed as 4.1 square miles and consists principally of woodland.

The lower compartment had reverted to the initial stages of the red maple swamp type, while the upper contained the entire ecological sere from the open marsh to the oak-hard maple forest type. Eight islands, varying in size from 0.21 to 1.24 acres, are located in the upper section. Each was forested with the mixed hardwood type in the 20 to 40 age class.

Construction of an earthen dike by the State Board of Fisheries and Game, using the original southern dike as the base, was completed during October, 1951. The dike is 821 feet long with a top width of 10 feet. The impounded area comprised 121 acres.

FIELD TECHNIQUES

Major floristic types were determined by a 50 percent strip cruise on the marsh and a 40 percent strip cruise on the upland. Cruise lines in the field were run by compass, and the data recorded in a formula patterned after

Arnold (1944). Permanent vegetative tally plots of 0.1 acre were placed within the major type. The number of plots was computed on the basis of a five percent area sampling with one plot as a minimum. Location of plots was determined by random selection of numbers from an overlay constructed for the entire area. A total of 47 plots were located and marked in the marsh.

Live trapping for all small mammals was initiated in July, 1952 and terminated in June, 1953. It was conducted during two periods, July-January and March-June. Large sized Sherman traps were set on north-south and east-west grid lines which were established at 500 and 200 feet intervals respectively. Trapping during the initial phase varied from two to six consecutive days, and was discontinued when the catch was drastically reduced. In the final phase, the traps were operated for five consecutive days at two week intervals regardless of catch. The traps were cleaned frequently during the trapping period, and were left open and exposed to the weather when the lines were not in operation. During the trapping periods the traps were checked once every 24 hours, generally during the early mornings. Sunflower seeds were used almost exclusively for bait. Mammals were toe marked and ear notched after data on sex, age and general condition were noted.

Live trapping specifically for rabbits was conducted only during October, 1952 with 46 double door guillotine traps.

A total of 204 small mammal live traps were placed at 50 feet intervals on parallel lines, 50 feet apart. Three lines transected the refuge from upland to marsh; three were laid out entirely within the marsh; and two crossed the eastern and western portions of the upper dike and three of the larger islands in the upper marsh. A minimum of eight traps was set in each major floristic type.

The traps were relocated when the marsh was flooded. The center of the new line was the intersection of the projected original line and the upland type. The traps were placed on parallel lines with the same spacing between lines and traps as before inundation. Minimum distance from the marsh edge to the upland type was approximately 100 feet in the denuded area, and required additional traps for adequate coverage. Where flooding did not occur, traps were undisturbed in their original positions.

Snap trapping was conducted during the period June 30 to July 17, 1953 for 2,418 trap nights. Lines were checked once a day for three consecutive days then moved to new locations. The traps were placed at 30 feet intervals, 30 feet apart, in three parallel lines following the marsh contour on the east and west borders. Islands were trapped in the same manner as the borders, but the number of lines varied with the width of the island.

White-footed deer mice (*Peromyscus leucopus noveboracensis*) were grouped into three age classes: immature, subadult, and adult as determined from pelage pattern, breeding condition, and size. Animals with more than one-half of the dorsal surface gray were considered immature. Those with more than one-half of the dorsal surface brown were subadults, and those with brown over the entire dorsal surface and white covering the ventral surface were designated adults. In a few instances where the condition of the testes and pelage conflicted, the animal was listed as adult. The sex of the short-

TABLE 1.—Animals marked before and after flooding

Species	Before Flooding Age and Sex of Marked Animals						
	Adults		Subadults		Immature		Total
	M	F	M	F	M	F	
Peromyscus leucopus	57	29	3	6	9	7	111
Microtus pennsylvanicus	16	11			1	2	30
Clethrionomys gapperi	1	2					3
Tamias striatus	3	4					7
Blarina brevicauda	1	3					4
Sorex cinereus	1						1
Glaucomys volans		1					1
Tamiasciurus hudsonicus	1						1
Zapus hudsonicus		1					1
Totals	80	51	3	6	10	9	159

Species	After Flooding Age and Sex of Marked Animals						
	Adults		Subadults		Immature		Total
	M	F	M	F	M	F	
Peromyscus leucopus	36	22	7	8	5	5	83
Microtus pennsylvanicus	1	4					5
Clethrionomys gapperi	2	2					4
Tamias striatus	10	3			2	1	16
Blarina brevicauda							0
Sorex cinereus							0
Glaucomys volans	1	1					2
Tamiasciurus hudsonicus							0
Zapus hudsonicus	3						3
Totals	53	32	7	8	7	6	110

tailed shrew (*Blarina brevicauda brevicauda*) was ascertained by internal examination of the reproductive organs.

OBSERVATIONS

Live trapping was conducted in all habitats before flooding. The total number of trap nights was 2,807 of which 1,676 were in the marsh habitat. The other habitats were trapped as follows: mixed hardwood—714; softwood-hardwood—345; new field or denuded area—72 trap nights. A total of 213 animals were captured of which 159 were marked and released. Forty-six percent (73 animals) of all the marked animals were caught and tagged in the marsh habitats.

The first flooding trial was initiated on August 6, 1952, but it was not completely successful. However, traps were relocated on the periphery of the anticipated water area. One trap was left in the marsh and set on a bog surrounded by water approximately six inches in depth. Two field voles (*Microtus p. pennsylvanicus*) were captured, one of which had been previously marked. Six deer mice were caught in traps removed to higher ground. A summary of the animals caught and marked before and after flooding is given in table 1.

Approximately 74 percent of the 194 deer mice marked in all habitats were retrapped during the study. Adult males showed a greater tendency to reenter traps than did the females (70 males, 38 females). Thirty-one percent of the 30 field voles marked and released were retrapped. Males were retrapped more readily than females (see table 2).

A total of 41 deer mice and 30 field voles were marked and released in the marsh before flooding. After flooding, only two adult deer mice were retrapped. Three adult female voles were captured in traps set on the upper dike in the fall after flooding. These animals were unmarked, and were captured in an area that had not previously yielded this species.

TABLE 2.—Retrapped animals*

Species	Sex and Age	Total	Times Retrapped	Average
Peromyscus	Adult Male	70	178	2.5
leucopus	Adult Female	38	122	3.2
	Subadult Male	5	10	2.0
	Subadult Female	12	34	2.8
	Immature Male	7	12	1.7
	Immature Female	10	21	2.1
Total		142	377	2.6
Microtus	Adult Male	7	11	1.6
pennsylvanicus	Adult Female	2	2	1.0
	Immature Female	2	3	1.5
Total		11	16	1.4

* 74 percent of the marked *Peromyscus* were retrapped at least once.
31 percent of the marked *Microtus* were retrapped at least once.

Three islands in the marsh that had been trapped before flooding were retrapped in December, 1952. Four deer mice and one shorttailed shrew were captured during this period. Seven deer mice, six jumping mice, 16 chipmunks, one short-tailed shrew and one flying squirrel were captured on the islands during the spring and summer trapping periods.

Snap trapping was more effective than live trapping in capturing shrews. Twenty-nine short-tailed shrews and 11 long-tailed shrews (*Sorex cinereus* and *S. fumeus*) were caught in 6,503 live trap nights. This is contrasted to 20 short-tailed and 12 long-tailed shrews caught in 2,418 snap trap nights. Their small size, which may enable them to escape, and their probable trap shyness may contribute to the difference between live and snap trapping results. A summary of the snap trapping data is given in table 3.

Mortality from trapping prior to flooding was attributed to the temperature extremes of summer and winter. Adult male deer mice had a 10.5 percent mortality as compared with 3.6 percent mortality for adult females. The mortality of the male was approximately three times greater in the fall as compared to six times greater for the female during the same period.

Mortality of adult male mice after flooding was approximately twice as great as that of female mice. The total mortality of all deer mice was 15.1

TABLE 3.—Snap trapping totals

Species	Adults		Subadults		Immatures	
	Males	Females	Males	Females	Males	Females
Peromyscus	37	23	1	8	9	6
Blarina	4	11				
Tamias	2	5			1	
Sorex		2		4	1	2
Microtus	3	2			1	
Clethrionomys	3	1				
Napaeozapus	1					
Zapus	1					
SEX UNDETERMINED						
Peromyscus	6		1		1	
Blarina	5					
Sorex	3					

TABLE 4.—Longevity of *Peromyscus leucopus*

Sex and Age	Av. No. of days between first & last capture	Av. No. of days between first capture & death	Combined Average
Adult Male	64.5 (31)*	78.5 (10)*	67.9
Adult Female	70.1 (20)	91.4 (7)	86.1
Subadult Male	140.0 (1)	0	140.0
Subadult Female	61.6 (5)	98.0 (1)	75.3
Immature Male	28.5 (4)	54.0 (1)	35.0
Immature Female	49.0 (2)	82.0 (1)	52.6

* Based on total number of observations between first and last capture and total number of observations between first capture and death.

percent. Mortality for all ages, species and sexes, as based on the data available, after flooding was 8.2 percent. Mortality for the entire trapping period was 15.4 percent.

Daily movements of deer mice by seasons (see table 6) was determined by measuring the distances between successive captures of those animals that were caught three or more times. The authors limited the data to three or more successive captures to reduce the influence of drift from surrounding areas. The average distance for all deer mice for the summer period was 105.3 feet. This may be contrasted with the spring season averaging 173.5 feet as based on ten observations, and the fall season averaging 139.5 feet as based on nine observations.

Longevity was determined by recording the deer mice that were captured more than one time with ten or more days between the first capture and death, or first and last capture. These data indicate that the adult males live

TABLE 5.—*Peromyscus leucopus* habitat utilization
(By age classes and by seasons)

Age Class (years)	Summer	Fall	Fall	Winter	Spring	Summer
A. 0-10	5.0	2.3	I N U N D A T E D			
B. Denuded Area	6.7	33.3	8.9		4.5	4.0
C. 0-20 20-40	8.8	10.6	9.8	7.7	2.7	4.4
D. 20-40 40-60	7.6	8.3	8.3		4.1	8.3
E. 0-20 20-40 40-60 60-80	8.7	9.9	9.5	7.7	3.4	5.3

A. Marsh; B. New Field; C. Forest; D. Forest; E. Total all forest types.

TABLE 6.—Mean daily movements by seasons of *Peromyscus leucopus*
(As based on three or more captures in different traps)

Age and Sex	Spring	Fall	Summer	Average/Year
Adult Females	86 (6)*	125 (3)	131 (10)	114 (19)
Adult Male	261 (4)	154 (6)	144 (19)	186 (29)
Subadult Female			103 (3)	103 (3)
Subadult Male			100 (1)	100 (1)
Immature Female			96 (2)	96 (2)
Immature Male			58 (1)	58 (1)
Average for all ages and sex	173.5 (10)	139.5 (9)	105.3 (36)	109.5 (56)

* All distances in feet. Numbers in parentheses indicate the number of observations on which measurements are based.

an average of 67.9 days (range of 10 to 262 days), and the adult female lives an average of 86.1 days (a range of 12 to 371days). The data are summarized in table 4.

Utilization index (the number of individuals caught, divided by the total number of trap nights, multiplied by 100) indicated that deer mice utilized the 0-10 year age classes (marsh type) more heavily before flooding in the summer than in the fall. In the summer, a utilization index of 5 was computed which is compared with 2.3 for the fall of the year. The utilization indices of the other habitats are given in table 5.

Increased usage of the older stands surrounding the marsh in the fall was proportional to decreased cover and food. There is no evidence that rising water contributes greatly to fall movements.

In the summer and fall before flooding, deer mice utilized most extensively the habitats with a canopy of 40 percent or more. Canopies with a density greater than 50 percent were the most desirable at both seasons. Types with a 60 percent canopy had an index of 9.7 in the summer and 18.6 in the fall; whereas, types with 70 percent and 80 percent densities had indices of 8.9 and 11.3 and 8.4 and 4.6 respectively.

Utilization indices for field voles were plotted in relation to various canopy densities for the summer before flooding. The majority of the observations were located in the 10 percent canopy density with a record of one each in the 50 percent and 70 percent canopies. The higher canopy densities were adjacent to the marsh edge. The greater proportion of animals were captured between the edge of marsh and upland types.

DISCUSSION

A computed sex ratio of 1.6 males to 1 female for all deer mice trapped is about the same as the findings of other investigators in other parts of the country (Johnson, 1927; Burt, 1940; Blair, 1940). The spacing and pattern of the traps, which differs in each investigation, may explain the discrepancies found between sex ratios. Townsend (1935) claimed that when traps are set in a grid pattern covering an area of an acre or more, the possibility of capturing more females with a smaller daily and seasonal cruising radius is increased. Traps set at widely spaced intervals are limited in the number of resident males and females that they may capture, while the capture of wandering males is increased.

Adult male and female deer mice had a higher trap mortality after flooding. The fall had the greatest mortality before flooding, and the spring had the greatest after flooding. Increased movement with the onset of the breeding season, scarcity of food in the early spring, and fluctuating weather conditions are believed to account for the increased spring mortality. Adult male deer mice had greater mortality throughout the year than the females. This may be accounted for by their greater numbers exposed to the decimating elements.

Various investigators have reported the home range of the adult male deer mouse as covering a larger area than that of the adult female. Burt (1940)

recorded the average home range of the adult female woodland deer mouse as 1012 square yards, and that of the adult male as 1312 square yards. The movements of the deer mice on Charter Marsh indicates that males have a wider cruising radius than the females.

Forty-one deer mice and 30 field voles were marked and released in the marsh habitat before flooding. Two marked deer mice were retrapped after inundation, and four unmarked field voles were captured in areas that did not yield this species before flooding. The percentage of retrapped animals in the study was 75 percent. Blair (1948) recorded that of the 26 deer mice that disappeared from his trap plots, only 7.7 percent were recovered by extensive trapping of the peripheral areas. He states that a greater percentage should have been retrapped if movements were responsible for the major loss. The larger number of retrapped animals at Charter Marsh indicates that more than the two marked deer mice should have been recovered during the post impoundment period if the animals migrated because of rising water.

Island trapping immediately following flooding did not yield any appreciable increase of animals on these islands. Moss (1942) found in his study that voles retreated to an island when the area became flooded, and were abundant through the first fall and winter. One observation on Charter Marsh indicates that voles are reluctant to leave their homes despite flooding. During August, in the midst of a flooding attempt, two voles were captured and released. They swam immediately to the nearest bog and disappeared in the vegetation. Under such conditions and depending on the extent of the flooding, a large percentage of the resident population would be isolated and perish. Wood (1910) reported that during spring floods on the Illinois River, voles were clinging to stumps that rose above the water. He states that it was probable that mice and shrews may escape in this manner. The conclusion that flooding must cause great mortality among small mammals because of exposure and their inability to escape by swimming long distances is confirmed by Blair (1939) who trapped a flood plain area after inundation for 225 trap nights, and on seven nights scattered throughout the summer with a yield of only one deer mouse. He found that wholly terrestrial species, confined to flood plains are virtually exterminated by extensive floods. Stickel (1948) found that a temporary flood of the Patuxent River did not adversely affect the small mammal population.

Blair (1948) constructed a survival curve for deer mice which is used as a basis for comparison of Charter Marsh data (fig. 1). The data obtained from Charter Marsh when not subjected to inundation displays a curve comparable with that of Blair's average July populations. These data depict a rapid drop before fall, and a more gradual decline thereafter. The curve constructed for the population of the marsh subjected to inundation is significantly different, and indicates that the population was destroyed as a direct result of flooding.

The longevity of deer mice as determined at Charter Marsh differs considerably from that found by Blair (1948). The adult males had an average life span of 67.9 days, and the adult females 86.1 days in comparison with Blair's 4.6 plus or minus 2.1 months. The difference is attributable to the paucity of data collected from Charter Marsh.
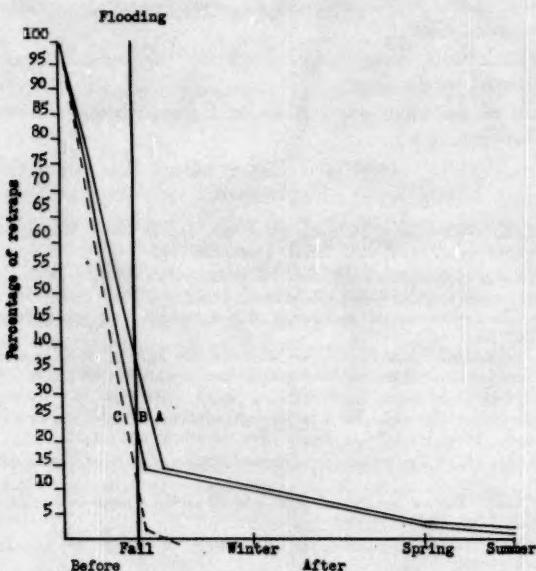
Fig. 1.—Survival curve for *Peromyscus leucopus*. A. Average of Blair's July populations for 1938-39 and 1940-41; B. Animals marked in all habitats and retrapped before and after flooding; C. Animals marked in the marsh—retrapped before and after flooding.

CONCLUSIONS

A large percentage of the small mammal population perished as a result of permanent flooding.

A total of 2,418 snap trap nights in the border area during June and July after flooding attempts yielded 16 marked deer mice and one redback vole for a ratio of marked to unmarked of 11.7 percent. No animal marked in the marsh habitat was recovered.

Deer mice utilized the 0-10 year age class (marsh type) more heavily in the summer than in the fall prior to flooding. After flooding this habitat was abandoned by deer mice.

Trap mortality was greater in the fall than in the summer, for both the adult male and female deer mouse before flooding. After flooding, mortality was higher in the spring than in any other season before or after flooding.

Approximately 74 percent of 194 deer mice marked in the entire study were retrapped. Two deer mice marked in the marsh before flooding were retrapped after flooding.

There was no marked increase in the small mammal population on the islands after inundation.

The animals with home ranges bordering the upland types were not adversely affected by flooding.

Sex ratios of deer mice was 2 males to 1 female before flooding and 1.6 to 1 after flooding.

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Food Consumption and Body Weight in the Masked and Short-Tail Shrews[1]

Peter R. Morrison, Marybelle Pierce and Fred A. Ryser[2]
University of Wisconsin, Madison

It is well known that smaller animals have higher specific metabolic rates and accordingly consume more food per unit of weight than do larger animals. This metabolic trend reaches an extreme in the smallest mammals, the long-tail shrews (Morrison and Pearson, 1947), and indeed, among naturalists shrews have long enjoyed the repute of having a voracious appetite (Seton, 1909; Jackson, 1928). However, this reputation has been largely based on fairly casual observations over short periods of time. Table 1 summarizes some reports from the literature on food consumption in various of the Soricidae. Much of this data is fragmentary or heterogeneous, precluding any firm conclusions as to true food requirements beyond that they appear substantial.

TABLE 1.—Food consumption in shrews according to various authors

Species	Body wt. g	Food	Consumption g/day	g/g day	Days	Reference
Sorex cinereus	3.6	worms, insects	11.7	3.3	7	Blossom, 1932
Cryptotus floridiana	5.0		5.5	(1.1)		Springer, 1937
Diplomesodon pulchellum	10.0	lizard, mouse	10-17	(1.3)	8	Hepner, 1939
Sorex palustris	10.0	meat, fish	10.3	1.0	4	Conoway, 1952
Sorex palustris		mice, snails		(2.5)	1	Svihla, 1934
Sorex araneus	11.0	meal-worms	6.8	0.62	88	Rorig, 1905
Blarina brevicauda	18.0			(0.3-0.5)		Hamilton, 1930
Blarina brevicauda		mice		0.7		Babcock, 1914
Blarina brevicauda		mice, worms, larvae	(16)	0.9	9	Shull, 1907

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Of the two animals considered here, the short-tail shrew (*Blarina brevicauda*) is a larger representative, but insectivores as a group show a higher metabolic level than rodents of comparable size (Morrison, 1948; Pearson, 1951). The other, the masked shrew (*Sorex cinereus*), may be considered at the lowest limit of mammalian size.

MATERIALS AND METHODS

Masked and short-tail shrews were trapped locally, and eight individuals of each species were maintained in moss-floored aquaria during October and November of 1952 for the duration of those experiments. Ordinarily these animals were maintained on whole mouse or rat carcasses which were supplied in excess of their requirements. For this study it was thought preferable to use a more homogeneous food supply. Five types were employed: beef liver, rat liver, whole newborn rats, earthworms and ground beef. A smaller number of preference observations were also made where two different foods were presented simultaneously.

There were two potential sources of error in measuring food consumption. First, desiccation losses could simulate consumption and second, food fragments could be scattered and lost. *Sorex*, in particular, like to drag off pieces of food. To prevent these losses, the food was securely wired to corks which were inserted in 10 cm long sections of pyrex tubing, 20 mm in diameter for *Sorex* and 35 mm in diameter for *Blarina* (fig. 1). The evaporative weight loss from control samples thus arranged was less than 0.1%/day, an amount considered negligible. The animals were weighed twice daily on a 100 gm, triple-beam balance to the nearest centigram (*Sorex*) or decigram (*Blarina*) principally as a control to insure that they were in weight equilibrium during the feeding experiments. The residual food was removed and weighed at the same times. Rates of consumption were calculated for the previous 9-15 hr. period as gram food per gram of animal per day (g/g day).
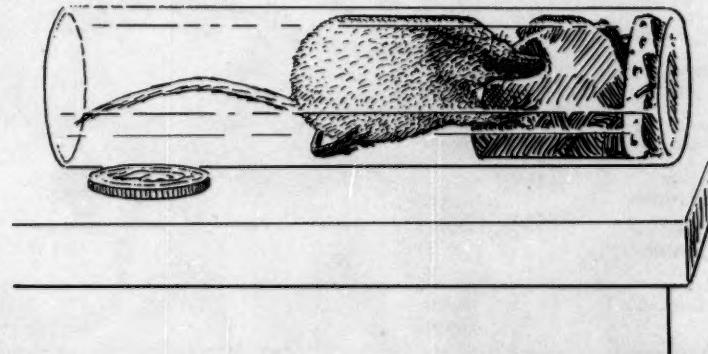
Fig. 1.—Sketch of experimental arrangement showing *Sorex* feeding inside the tube. The amount of beef liver pictured represents about one day's consumption. Usually a glass tube open at both ends was used for easier access to the food.

Fig. 2.—Representative experiment showing feeding frequency and duration during a single day in *Sorex* (5/27/53). Arrows indicate food supplied.

In recording feeding frequency (fig. 2) in *Sorex* the food (liver) was not enclosed in tubes since amounts were not measured, but rather, fastened inside a small screen cage. This was suspended by light rubber bands and to it was attached a vibration-sensitive, electrical "pick up." The information from this unit was taken down on a continuous roll, Esterline-Angus, ink-writing, operation recorder. A feeding "response" could be easily distinguished from casual disturbance to the unit by its longer duration. Only activity which continued for at least a half minute was tabulated as feeding. Excess food was always supplied, but if changed too infrequently it apparently became unavailable to the animal due to surface drying.

RESULTS

Table 2 describes the variation in weight of individual *Sorex*. Values for the coefficient of variation (100 σ/W) range from 2.4 to 5.4% and average 3.6%. Although the body weight was thus ordinarily quite constant, under abnormal or unusual circumstances considerable changes were observed due to restriction of feeding. This effect was seen in some animals which never adjusted to trapping or captivity and apparently starved to death. It was also seen in metabolic experiments where animals were confined in small screen chambers and exposed to temperatures of 5 to 30°C (Morrison, Ryser and Dawe, 1953). Under these circumstances weight losses were always observed

TABLE 2.—Body weight and its variation in individual *Sorex*

Indiv. No.	Aver. Wt. g	Standard deviation		Values
		g	%	
3	3.27	0.127	3.9	22
4	3.32	0.178	5.4	7
5	3.66	0.153	4.2	10
6	3.35	0.101	3.0	30
9	3.63	0.110	3.0	9
10	2.92	0.070	2.4	9
11	2.98	0.086	2.9	12
12	3.70	0.138	3.7	9
(8)	3.35 ± 0.30	0.120	3.6	108

TABLE 3.—Body weight and its variation in individual *Blarina*

Indiv. No.	Aver. Wt. g	Standard deviation		Values
		g	%	
5	27.9	0.73	2.6	42
6	20.6	0.49	2.4	44
7	22.0	0.90	4.1	27
8	21.3	0.79	3.7	18
9	21.8	0.47	2.2	5
10	20.0	0.74	3.7	13
11	20.5	0.71	3.5	11
(7)	22.0	0.69	3.2	160

although an excess of food was available. The mean loss in 11 such experiments of 7 hr. duration was 0.24 g or 6.8% of the initial body weight. Such losses were not observed in similar experiments where the animals were not exposed to cold. Following the metabolic experiments, after the animals were returned to the terraria, weight was regained rapidly, usually to exceed that at the beginning of the experiment. In seven cases an average weight increase of 0.36 g or 11.0% was observed within 3 hrs.

Comparable data for *Blarina* comprising 160 values are summarized in table 3. Except for one 28 g animal these formed a homogeneous group weighing from 20-22 g. The average standard deviation for these individuals was 0.69 g or 3.2%, a value quite comparable to that noted above in *Sorex*.

Food consumption data for *Blarina* representing 168 values at 25° and 30 values at 5°C on three foods are summarized in table 4. Average values for beef and rat liver are quite comparable (0.4-0.6 g/g day) but the intake of whole newborn rat was substantially larger (0.92 g/g day). Consumption

TABLE 4.—Food consumption in *Blarina*

Food type	Temp. °C	Body wt. g	Values	Feeding g/g day
Newborn rats	25	28*	2	0.55
Newborn rats	25	21	17	0.96
Rats	25	22	19	0.92
Rat liver	25	28	19	0.42
Rat liver	25	21	14	0.60
Beef liver	25	28	22	0.43
Beef liver	25	21	94	0.62
Liver	25	23	149	0.56
Beef liver	5	28	3	0.52
Beef liver	5	21	11	0.77
Calf liver	5	28	4	0.62
Calf liver	5	20	12	0.73
Liver	5	22	30	0.71

* Blarina No. 5 which weighed 27.9 g was substantially larger than the other 7 shrews which ranged from 19.2 to 22.0 g.

values at 5°C were definitely higher (+27%) than at 25°C. The single 28 g animal had a lower food intake than the 7 other 19-22 g animals at both 5° and 25° (—24 and —30%).

Comparable data for *Sorex* comprising 83 values are given in table 5. Again, values for rat and beef liver are similar, but very much larger amounts of newborn rat were consumed by two individuals (1.5x). Other animals had almost the same consumption of liver and newborn rats. This data has been grouped into three classes according to the weights of the animals, but sufficient values for comparison on the high and low weight classes are only available for the beef liver series. Here a definite correlation is seen with higher consumption rates (as g/g day) in the smaller shrews. In one case even the absolute value (g/day) was higher, with *Sorex*-11 (2.92 g) consuming an average of 5.3 g of liver in a day as compared with 4.5 g for *Sorex*-5 (3.66 g). Food consumption in the cold was increased substantially (+73% for *Sorex*-11 eating newborn rats). Further consumption values in the cold are given in table 6 for mixed diets. This table, however, is primarily presented to show differences in food preference, which range from an extreme of 13:1 for newborn rat:worm to almost identity, 1.2:1.0, for beef liver:ground beef.

The representative record of feeding frequency in *Sorex* during a single day (fig. 3) shows numerous, short periods of feeding activity. Over a 96-

TABLE 5.—Food consumption in *Sorex**

Food type	Temp. °C	Body wt. g	Values	Feeding g/g day
Newborn rats	5	2.98	5	2.99
Newborn rats	25	2.98	2	1.73
		3.31	13	2.50
		3.32	2	1.31
		3.66	2	1.43
Newborn rats	25	3.3	19	2.17
Worms	25	3.35	5	3.84
Worms	25	3.4	5	2.40**
Rat liver	25	2.92	1	1.61
		3.32	20	1.72
		3.66	3	1.27
Beef liver	25	2.93	7	1.76
		3.31	15	1.50
		3.65	13	1.42
Liver	25	2.93	8	1.74
		3.32	35	1.62
		3.65	16	1.39
Liver	25	3.3	59	1.58

* Values measured twice daily and rates as g/g day calculated over the elapsed time.

** Values corrected for weight of dirt in the gut (37%).
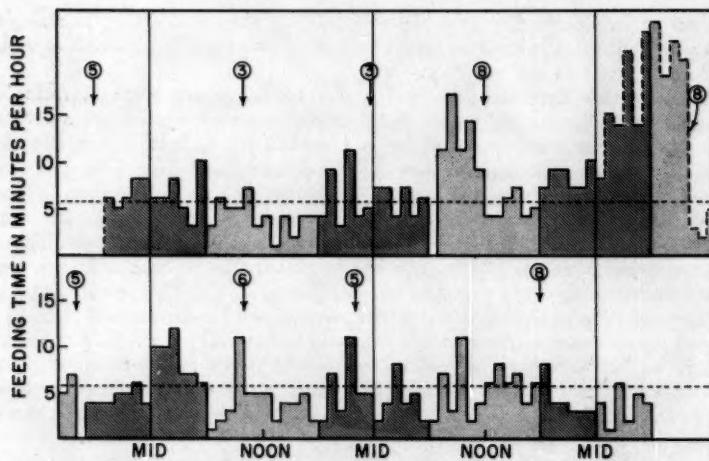
Fig. 3.—Bar graph showing feeding intensity as min./hr. in *Sorex* over a week long period: above, 5/22-25; below, 5/26-29. Dotted line shows average rate exclusive of the hyperactive period (upper right) caused by failure to renew the food supply. Dark and light hatching indicate P.M. and A.M., respectively; circled values indicate g of food supplied.

hour interval, 386 1-minute periods (*i.e.*, 0.5 to 1.5) and 61 longer periods of 1.5-3 minutes were recorded. This represents an average of 4.8 feeding periods per hour or one every 13 minutes. Over the entire week-long experiment only two 1-hour periods without any feeding were noted. The maximum observed frequency in an hour was 17, or an average of less than 4 minutes between feedings. The fractional feeding time (as min./hr.) is shown in fig. 4 over the entire experiment. The average rate was 5.4 min./hr. or 9%. No difference in this value was seen between night and day.

TABLE 6.—Food preference in *Sorex*

Food choice	Expts.	Temp. °C	Feeding g/g day	Ratio g/g	Ratio cal./cal.
Beef liver worms	2	25	1.55 / 0.42	3.7	13
Newborn rats worms	2	25	1.66 / 0.12	13.8	35
Newborn rats worms	1	5	1.86 / 0.12	15.5	39
Newborn rats Ground beef	3	5	1.69 / 0.21	8.0	5
Beef liver Ground beef	2	5	1.69 / 1.40	1.2	1

DISCUSSION

Because of their high metabolic intensity one might suppose that *Sorex* was more "critically balanced" than larger mammals, and consequently would show greater fluctuation in various regulated levels. As regards weight this is certainly not so. The average standard deviation of 3.6% observed in *Sorex* is little more than the value of 3.2% seen in *Blarina* or of 3.2% observed in the white mouse (Chevillard, 1935) and 3.0% in *Microtus pennsylvanicus* (Morrison, 1948). Accordingly *Sorex* maintained its weight within as narrow limits as other mammals which are 5- to 10-fold larger. The variation between mean weights of these individuals ($\sigma = 9\%$) was substantially smaller than that we have found in wild-trapped populations of Alaskan *S. cinereus* ($\sigma = 19\%$).

Since the values for the several types of liver used as food compare closely and since a much smaller number of measurements were made on other food types, liver will represent the most reliable food index. The observed consumption of liver in *Blarina*, 0.56 g/g day, lies midway between Hamilton's estimate and the values of Babcock and of Shull for mice as food (table 1). At 1.22 kcal/g of liver[3] this represents 0.68 kcal/g day. This is about 13% more than the value of 0.60 kcal/g day (5.3 cc 0_2/g hr.) from the mean daily oxygen consumption (Morrison, 1948; Pearson, 1947). The mean value for liver consumption in *Sorex* was 1.58 g/g day or 1.93 kcal/g day. This is 8% higher than the average caloric requirement of 1.78 kcal/g day (15.8 cc 0_2/g hr.) determined as oxygen consumption measurements (Morrison & Pearson, 1946). The occurrence of very frequent feeding periods correlates well with the almost constant activity pattern observed in oxygen consumption studies.

The different consumption rates for the several food-stuffs (presented individually) appears explainable in simple terms of energy content. The worms contained more than one-third weight of dirt and their tissue represented only 12% of solids. If these factors are taken into account, $3\frac{1}{2}$ g of worm ("on the hoof") provide the energy equivalent of 1 g of liver. In the experiment on *Sorex* (table 5), although almost 4 times the body weight in worms was eaten, this is about a third less than the required amount, and the shrew lost weight ($3.27 \rightarrow 2.97$ g) and died. The newborn rats which were eaten bones and all, must also represent a less concentrated energy source. Maintenance consumption levels for this food were 1-55% higher than for liver.

When other food was present the "low grade" worms were hardly touched (table 6). However, newborn rats were definitely preferred (5-8x) over the more concentrated ground beef. One cannot say whether *Sorex* is merely showing a taste preference or if it may "recognize" the superior nutritional quality of the newborn rats. Average preference ratios (Morrison and Tietz, 1953) for the four foods consumed in binary experiments in terms of the relative amounts were as follows: newborn rat: liver: ground beef: worms = 100:26:18:7 (g) = 100:37:30:3 (cal).

The correspondence between oxygen consumption and food consumption

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[3] This is 0.90 of the value of 1.36 kcal/g for beef liver given by Wooster (1954), the difference representing a lower dry weight in our material (27%) as compared to his "standard" liver (30%). In view of liver's ready digestibility the metabolizable energy equivalent should be very close to the calorimeter value.

is even closer when one considers the conditions under which oxygen consumption was measured. The metabolism chambers limited activity more than the larger aquaria in which the animals were maintained during the feeding experiments. In addition, animals in nature must be considerably more active in searching out and capturing their own food, and their natural energy and food requirements will be substantially higher. The energy cost of thermoregulation must be added to this if the animals venture below thermal neutrality (*ca* 25°). The metabolic rate is increased 2-2.5 fold at 0-5° (Morrison and Ryser, 1951; Morrison, Ryser and Dawe, 1953). Even when the animals were protected by nesting material during inactive periods, food consumption was 27-73% higher (tables 4 and 5). Accordingly, values for food consumption approaching the body weight for *Blarina* and 2½ times the body weight for *Sorex* are probably not unreasonable estimates of daily requirements in nature.

SUMMARY

Food consumption was measured in 8 individuals each of 3 g *Sorex cinereus* and 21 g *Blarina brevicanda*. Average rates at 25° were 1.58 and 0.56 g/g day for beef liver. When expressed as the energy equivalent these are about 10% higher than those derived from measurements of oxygen consumption. Newborn rats were preferred over liver, ground beef and worms in that order. In *Sorex* feeding activity could be as intense as 17 periods per hour, but averaged 4 periods per hour, and intervals between feeding of as long as an hour were observed only rarely. In both species the constancy of the body weight was comparable to that in mice ($\sigma = 3.2\text{-}3.6\%$).

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Notes and Discussion

An anomalous appendage on the carapace of the crayfish Orconectes rusticus

A specimen of *Orconectes rusticus* (Girard) collected in the summer of 1955 was found to bear an anomalous appendage attached to the carapace similar to the case recently reported for the American lobster (Dexter, R. W. 1954. Ohio J. Sci. 54:192-194.). The crayfish was collected by Roger Meola, student at the Stone Institute of Hydrobiology, on June 29, 1955, while seining in the Pond of the Portage River about one mile upstream from its mouth on the southwestern shoreline of Lake Erie. During examination of the specimen by the class in Invertebrate Zoology, a small biramous appendage was discovered attached to the right side of the carapace. It was a male specimen with a total length of 83 mm from tip of the rostrum to end of the telson. On the right side of the carapace, at the edge of the areola, was a slit-like wound 5 mm long running parallel to the cervical groove. The wound had healed and had produced a small biramous appendage. The exopodite measured 2 mm square with a fringe of 12 hairs 0.7-0.8 mm. long. The endopodite measured 0.6 mm broad and 0.5 mm long and was fringed with 4 hairs 0.6 mm long. See fig. 1. Probably this anomalous appendage was traumatically induced just prior to or at the time of the last molt when the carapace was still soft and the hypodermis beneath was still active in growth. There is now evidence from both a marine and a freshwater crustacean that injury to the

Fig. 1.—Biramous appendage on carapace of *Orconectes rusticus*.

hypodermis underlying the carapace may initiate the growth of a biramous appendage.— RALPH W. DEXTER, Kent State University, Kent, Ohio, and the Stone Institute of Hydrobiology, Put-In-Bay, Ohio.

Pehr Kalm's Account of the North American Rattlesnake and the Medicines Used in the Treatment of Its Sting.

Translated and edited by Esther Louise Larsen[1]

Pehr Kalm, the first trained scientist to visit North America, arrived in Philadelphia in September, 1748, for a two and one half year visit. A student of Linnaeus, his mission was to search for plants of sufficient economic significance to merit their introduction into Sweden and Finland, and to supply scientific information to Linnaeus and to fellow members of the Kongl. Svenska Vetenskaps Academien. Kalm, with his scientific training, wide interests and natural curiosity, left for posterity records not only of the natural phenomena which he observed, but also a detailed account of the cultural history of the period. His journal *En Resa till Norra America* (A Journey to North America) published in three volumes in Stockholm, 1753-1761, is invaluable to the student of colonial history, because it includes details which the chronicler of the familiar scene tends to ignore.

The results of Kalm's scientific observations were published in a series of articles which appeared in Kongl. Svenska Vetenskaps Academiens *Handlingar* from 1749 to 1778. In them he discusses agriculture, climate, animals, insects and the economic value of trees, shrubs and herbs together with their characteristics and medicinal uses. This series includes an article which is here translated under the title *An account of the North American Rattlesnake and the medicines used in the treatment of its sting.* It was published in three parts[2] in the *Handlingar* 13:308-319. 1752, 14:52-67, 185-194. 1753, under the titles *Berättelse om Skaller-Orm, samt de läkemedel som i Norra America brukas emot dess stygn* and *Slutelig berättelse om Skaller-Ormen, i synnerhet om botemedel emot hans bett.*

During the eighteenth century, it was often difficult to distinguish fact from fiction in the natural sciences. Kalm, a keen observer and an accurate reporter, was skeptical of much information given him. If the information came from persons whom he considered reliable, he recorded the source. But, his skepticism was evinced by such statements as: "I have never observed this reaction myself and I find it difficult to believe" or "The above information was substantiated by reliable men who almost dispelled my doubts as to the veracity of these tales."

The information on snakes in Kalm's journal, which is in part, credited to Cadwallader Colden, caused considerable ill will. The situation is discussed by his son David in a letter to Benjamin Franklin dated November 30, 1772.[3]

"I have lately got the Annual Register for 1771, One of the first Things I fell upon was the Abstracts from Mr Kalms account of his Travels in America I was much surprised with a wonderfull story he tells from my Father, of a black Snake that attacked one of our Servants, for I never heard the Story in the Family, indeed the date he gives it is within my own Memory—My Father cannot immagine how Mr Kalm came to father such a Story upon him, for no such Thing ever happend in our Family, or to any one that he ever heard of, the Traveller could not have got it from him. . . . —I had two opportunities a Year or two agoe, of examining the black Snake facinating a Bird; which Mr Kalm does not omit some [? from his] wonderful Tales. In both the Cases which I saw, I found the Bird was far from being in Love with the Snake, that she was doing her

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[3] Cadwallader Colden Papers, The New York Historical Collections, VII. 184. 1923.

utmost to drive him away from her Nest, putting her own Life into his Jaws to save her young Brood. I calld several Persons to examine the first of these Encounters which I saw; they all agreed that the Bird must be enchanted but alterd their Opinion as soon as I shewd them the Nest and the young Birds. I really beleive there is nothing more in all the Tales we are told of these Inchantments." It is interesting to compare the information in this letter with that which had been published twenty years earlier by Kalm in his article on the rattlesnake. He was meticulous in his own observations, but he was sometimes taken in by the folk lore of the period.

There are about twenty kinds of snakes in North America; some of these are poisonous. The rattlesnake is the most dangerous of the poisonous snakes. Instantaneous deaths have been recorded in cases where the snake bite was deep enough to reach the veins of the heart; however, such instances are rare. Those who are struck usually live for minutes, hours or even days. If proper medication is administered, the victim undergoes the ordeal and in time recovers.

The American savages, who live by hunting and are always running to and fro in the forests, have been most subject to the fangs of this dangerous snake. They have learned, of necessity, to use miscellaneous herbs and remedies in order to save their lives when they are struck. Europeans, since their recent arrival to the New World, have been forced to study and expand the knowledge of the savages.

During my American trip, I sought to become familiar with the medicines which had proven to be efficacious in the treatment of the bite of this dangerous snake. I shall present the information which I collected, in order that we may try the medicines available to us for the treatment of bites from our snakes. A knowledge of botanical relationships will make possible the investigation of those of our plants which are most closely related to the American medicinal plants involved. In order that the value of these cures be more fully understood, I shall give a brief account of the rattlesnake. The report, which I shall make, is based almost entirely on notes made during my travels. Little had been published previously. For those who wish to know what has been written on the subject, I shall list the books which I consulted.

In North America, the English call this snake the rattlesnake, that is *Skaller-Orm*. The Swedes, who live there, use the name *Rattle Slang* which they undoubtedly got from the Dutch. The French use the name *Serpent à sonnet*, the Germans *Rattle Schlang* and the Iroquois on the Mohawk river *Onegánsi*. In Sweden we use the translation *Skaller-Orm*.

An excellent colored illustration of this snake is given in Mr. Catesby's work *The Natural History of Carolina* vol. 11 p. 41. tab. 41. No artist can reproduce the burning brilliance of the snakes eyes when it is angry.

A description of this snake is given by Mr. Catesby in Amaen. Acad. vol. 1 p. 297 of Linnaeus. To this description, I add the following:

1. We killed one with 173 abdominal segments (*segementa abdominis*) and 26 caudal segments (*cauda*). The count was carefully made and checked. The snake was 7 2/3 qvarter[4] long, exclusive of the rattles on the tail of which there were seven. The snake, at its thickest part, was 1 inch 9 geom. lines.

2. He does not have two fangs (*dentescanini*) in his upper jaw as other snakes do, but several, four of these are almost equal in size, there being two on either side of the upper jaw inside the mouth. These fangs are long and sharp, like the sharpest awl or sewing needle, and can be pulled in or shoot out like cat's claws. Near the roots of these fangs are several smaller fangs which have not yet developed. The snakes which I dissected had 10-12 abortive fangs, 5-6 being on either side of the palate. The Creator, doubtless, has arranged it thus, so that the snake will not be without a weapon. If its fangs are broken, others replace them. Mr. John Bartram, a farmer in Pennsylvania, has discussed this fact in *The Philos. Transact.* n. 456. p. 358. The smaller fangs are just as sharp as the larger ones, but are nearly buried and remain covered until they are needed. If the root of a large striking fang is pressed, a quantity of green juice drips out of the end.

The snake is usually 3 to 4 feet long. The largest one I saw was 6 feet long and as thick as the calf of a man's leg. Usually they are as thick as the wrist.

In North America these snakes are found in Florida, Georgia, Carolina, Virginia and Pennsylvania. They are also found in New York, New England and Canada. Their

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[4] A qvart equals 1/4 alm or about 6 inches.

northernmost limit in Canada is a mountain near Lake Champlain called *Roche fendue* about ten French miles north of Fort St. Frederic about midway between 44° and 45° lat. Their northernmost limit in New England is the Merrimac river between 43° and 44° lat.

Formerly there were large numbers of these snakes in New Sweden as well as in other parts of North America now occupied by Europeans; however, they have nearly been exterminated. Now they are largely found in the high Blue Mountains,[5] or far inland, but they are still seen in European settlements occasionally. Many old people born in America have never seen a rattlesnake. In all my travels, I saw only 3 living specimens. I frequently heard them in the nearby thicket, but, it seemed inadvisable to pursue them.

The rattle, which is a series of hard cartilaginous rings fastened to each other, is located at the end of the tail. When the snake is approached, the head and tail are elevated above the coiled body. The tail shakes the rattles, producing a sound not unlike that of the humming of a spinning wheel when heard at a distance.

In the autumn, when it begins to get cold, they congregate in their winter lair, crawling deep into the ground. Many hibernate in one place, where the intense cold can not reach them. It is said that they make deep holes in the ground, gnawing away the soil, so that it caves in like an abandoned cellar. In the spring when the soil is bare and bathed by sunlight, the snakes crawl up and warm themselves during the day; but in the evening they crawl back again. This they continue to do until no night frosts occur. They then go away traveling here and there. The North American Europeans locate the lairs when these snakes come out en masse. They are still sluggish and can easily be killed while sunbathing. An old Swede, who came upon such a location, killed 16 snakes with one shot. Another Swede went out one spring morning, and came upon a hillside completely covered with rattlesnakes sunning themselves. He cut himself a stick and quickly killed between 60 and 70 snakes. He was finally forced to leave, because of nausea, due to the vile stench emitted by the angry snakes.

They also hibernate in porous mountains. I heard an account of a New Englander, who built his house into the side of a mountain, so that it formed one wall and part of the fireplace. An unusually large fire was laid in the fireplace one winter night. After the fire had been kept for some time, the snakes in the mountainside were liberated from hibernation and came crawling forth into the house. The entire family, man, wife and children, awakened by the rattling of the snakes, took to the rafters, where they were forced to stay until daybreak.

These snakes prefer the high forested mountains in the summer. During hot weather they invade woodlands and meadows. Stony mountains are preferred, particularly those composed of limestone. In the vicinity of the great Niagara waterfall where the mountains are composed of limestone, these snakes are numerous, in spite of the fact that they are constantly being killed on the trail between the lakes Ontario and Erie when commercial travel is heavy during the summer. Large numbers are killed in the spring, when they come out to sun themselves, and scarcely a summer day passes without two or three being killed on the trail.

During the summer these snakes are most apt to be found in the following places: (1) Near a fallen tree in the woods or in the sunlight. One should, therefore, be careful in traveling through the forest, not to step on such a tree or to climb over it, but to walk around it at a safe distance. If it is necessary to cross the trunk of a fallen tree, one should not step near to it in order to climb up or down. It is best to jump up onto the tree from a safe distance. Snakes frequently sun or rest under or near a fallen tree, and can easily strike anyone coming near to them. Savages, who constantly travel about the forests, never step on old fallen trees or over them, but always walk around them. (2) The rattlesnakes like southern exposures of hills and mountains and locations near springs or spring fed runs. They are clumsy and slow, and unable to overtake their prey. They choose to live where frogs are plentiful, and where other animals come to slake their thirst.

The age of the snake is thought to correspond with the number of rattles in his tail.

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[5] Apparently Kalm used the term "Blue Mountains" for all the mountains in the eastern part of the present United States. "These mountains which the English call the Blue Mountains, are of considerable height and extend in one continuous chain from north to south, or from Canada to Carolina."—A. B. Benson, ed., *The America of 1750; Peter Kalm's Travels in North America,* 1:65 (New York, 1937).

One rattle is said to be produced each year. Formerly snakes were found with as many as 41 rattles. Among my contemporaries I found one who in his youth claimed to have killed a snake which had 31 rattles. Others reported having seen as many as 20 rattles. Young snakes rarely have more than one. Most of the snakes now killed in the English Colonies have rattles varying in number from 1 to 12. It would seem that they are being destroyed at such a rate, that they do not have a chance to reach a great age.

The snake usually rattles a warning in the distance as a person approaches; but he may sometimes strike without warning.

Some consider the rattle a warning, others feel it indicates anger and malice.

I have noticed that the snake rattles when anything is thrown at it, but if one turns and walks off, the snake crawls away. If it is again frightened by a missile, it will rattle again. The snake which is not afraid does not rattle, but lies still until it is in a position to strike effectively. The rattler is quite fast when the sun is shining, but sluggish when it is raining. It is then dangerous to go where the rattlers are plentiful, because they may strike without warning. It is quite possible that snakes rattle during rainy weather without being heard, since wet rattles may not produce sound. Savages dislike traveling through the forests during rainy weather, because of danger from snakes or because of the difficulty of traveling through wet brush. The savages have no paved roads.

Savages say the snake does not rattle when he means mischief, but bites without warning.

Although I have seen many dead rattlesnakes, I have rarely seen one with its rattles. Perhaps they are valued as trophies or souvenirs. I have no idea why.

It is generally believed that rattlers travel in pairs. If one is encountered, another is thought to be nearby.

They travel slowly, thus one need not fear being overtaken.

The rattler does not run away, but waits to defend himself. If he is surprised he may retreat, but as soon as possible he stops and coils, holding up his head and tail. He gives his alarm and stares at his pursuer with burning eyes. If he is coiled when discovered, and he usually is, he will not move from the spot, but prepares to defend himself. I have noticed that he gives some kind of warning. If I approach quickly, riding or walking, and he is in my path, he will coil and begin to rattle with his eyes fastened on me. If I stop and turn away pretending not to see him, he stops rattling and disappears into the brush or dense thicket. If I turn about quickly and face him, he will again coil and rattle. If I look away and pretend not to see him, he again looks for shelter.

He never pursues, since he is much too slow. Now and then one hears tales of persons screaming in terror, because a snake had pursued them and they were barely able to escape. Surely they have mistaken the black snake for the rattler. During the mating season the black snake, which is one of the longest snakes in North America, attacks anyone he meets or anyone who attacks him. If a person attempts to escape, the black snake will give chase. Should he overtake the victim, he winds himself around his legs and trips him. It is fortunate that his bite is not dangerous and no worse than a small knife wound. He is the thinnest of all the snakes I have seen. It takes quick footwork to get away from him. He shoots out of the bushes like an arrow and there is no time to see what kind of snake he is. Everyone in America fears the rattler; so the natural tendency is to flee.

The rattler is a fair swimmer, traveling nearly as fast in water as on land. In order to be lighter while swimming he appears to have inflated himself and he floats like a bladder. It is unwise to attack a rattler as he swims, for he can easily throw himself into a boat. Such instances have been reported by reliable persons.

The rattler emits a repulsive odor when sunning or when angry. Even though he may not be heard, his presence is sometimes detected by odor alone. At times the stench from these creatures is almost unendurable. Horses and cattle nearly always detect the rattler by his odor. They snort when one is near, and quickly go around it. When the wind is in the wrong direction, the rattler is not easily detected. One day my horse came so close to a snake, that it might well have struck me in the boot or the horse in the leg.

The rattler is peculiar in that he usually does not injure a person unless forced to defend himself. I have heard of individuals stepping on coiled rattlers, while walking barefoot through the forest. Strolling along they remained wholly unaware of danger, until startled by the sound of the rattle. Some tell of having stood barefooted near the head of a coiled snake. An old Swede, carrying a load of dry leaves to a fire, suddenly

became aware that his load contained a coiled rattler which was looking him square in the eye. He was unaware of the snake's presnce, until it rattled. Needless to say, he quickly disposed of his load. According to the old man, the snake was so close it could have struck him in the face. Other persons, while traveling through the bushes, have stepped on a snake; then, thinking they heard a bird in the bush, bent over to see what manner of bird it was, and if it might be captured. Instead of a bird, there lay the snake in striking position, yet it did not strike. A snake has been known to crawl over sleeping persons without harming them. Such indifference can not be relied upon, for there are times when he strikes without provocation. After having eaten a squirrel or any other small animal, he is satiated and usually will not strike, unless he is touched. However, when he is hungry, he is ill tempered and dangerous. He is then ready to do damage to anyone who approaches. He is also nasty during rainy weather. The savages say that he rarely ever strikes during the month of July.

The rattler always coils before striking. When stretched out he can do no damage, and a foot can be placed next to his head without danger. However, it pays to be cautious. He may be a clumsy traveler, but he is agile in coiling, and is quickly in a position to strike.

The rattler can strike the greatest distance of any North American snake, but this distance is limited to one half the length of the body. In reaching out to strike, the snake must brace itself with the lower part of the body.

The rattler is cunning. If he is teased with a cane, he ignores it, and tries to strike the foot or leg. The rattler does not coil, unless there is some chance of his reaching the prey when he strikes.

Death sometimes occurs minutes after the snake has struck, but the victim may live for a long time. He may even survive, if suitable medication is used in time. The symptoms of the poison have been described by others. For example, the victim, when bitten on the foot, experiences no more discomfort, than if he had been pricked by a thorn. Sometimes the victim is blissfully unaware of the nature of the "thorn," until symptoms of the venom, such as faintness and swelling, occur. He then realizes what he brushed into. The bite, when examined, shows two small holes very much like those made by a needle. The victim becomes nervous, faint and has difficulty breathing. The wound swells; the victim develops an insatiable thirst; and aching develops in the region of the heart. If thirst is slaked by drinking water at this time, death may result. The tongue swells, and eventually becomes so large that it fills the entire mouth and turns black. In such a case, poisoning has gone far, but recovery is possible. The body becomes mottled. This gives rise to the belief that the victim takes on the color of the snake. If help is not forthcoming, the patient dies.

Under proper treatment the patient may recover, but his skin loses its natural color, and becomes yellowish. He may be disfigured for life, because of mottled skin, which is caused by the poison remaining in the system.

The victim, no matter how complete his recovery, has a yearly recurrence of discomfort. Bodily aching and swelling occur each year at about the time of the original poisoning. *Aristolochia*, which is used in the treatment of these cases, will be discussed later.

In Pennsylvania, a Swede by the name of Carl Låck (a grandson of Låckenus, who is mentioned in *Campanii Beskrifning öfver Nya Sveriget*, and who was the last clergyman sent to that country while it still belonged to Sweden) told me, that during his youth while hunting, he was about to step over a fallen tree, when a rattler lying on the other side struck at him. He ran in terror, but was so frightened, that he got sick and had to be helped home. For 14 days after the encounter, he was ill. Each day at the hour he had been frightened, he went to bed with a dreadful headache and backache, although before and after that hour he was perfectly well. He assured me that the snake had not bitten him.

Animals, which have been cured from the poison of this snake, have a recurrence of the symptoms each year. A reliable man from New Jersey told me that his dog was bitten by a rattler. A decoction made from the root of *Aristolochia* was given to the dog, who was cured, but became sick just a year later, and had to undergo the same treatment. Later the dog was bitten again and treated with the same decoction. However, a year after the last bite, the after effects of the venom were so great, that the dog got sick, dizzy and mad, and finally had to be shot.

When several riders pass near a snake lying close to a trail, he may remain quiet if

they ride on, but the last horse may be bitten. The same is true, if several persons follow a narrow trail. The first to pass may step right over the snake, but he is apt to strike the last one.

If a rattler is induced to strike a new hickory cane, the venom shows up as a green liquid. The venom does not run down, if the cane is upended.

Cows and horses frequently die when bitten, but dogs are more resistant and often recover. Dogs have been known to survive as many as five bites, although they may have been dreadfully sick. Dogs have also been known to succumb shortly after being struck.

Boots are not necessarily a protection. The fangs of the rattlers are long and sharp and may penetrate the boot, close to the foot or leg. This is unlucky. It is safest to wear wide sailor's pants, which come down to the shoes. If the rattler strikes the cloth of the pants, it buckles or wrinkles, making the strike ineffectual. Therefore loose pants are safer than boots.

While in America, I often heard the tale of the English farmer, who was wearing boots when struck by a rattler, and remained unharmed. Later, while greasing his boots, his hand received a cut like a knife wound. It began to swell and smart. The rattler's fang had remained in the leather, and the man ran it into his hand, as he rubbed the boot. Proper medication could not be obtained. The hand swelled greatly; the poison went up to the heart, and the man died. The fang which pierced the hand was said to have reached the bone. It is considered dangerous to wear boots which have been struck by a snake, because the fangs usually break off and remain in the leather.

Since my return to Sweden I have tried to strike a cat with fangs which I removed from the mouth of a rattler in America. The cat was not affected. American savages use the fang as a lancet in blood letting. It should be noted that fangs are washed clean of all poison before they are used thus.

Dr. Colden, a learned naturalist in New York, told me of the case where a rattler had struck a boot. The fang did not penetrate the boot; however four days later when it was pulled on, the fang scratched the leg. The resulting pain was such, that it was necessary to use the strongest antidotes to stop it.

The rattler feeds on small birds, frogs, squirrel and rabbits. Mink has also been found in its stomach. The mink lives in the water like the otter, and resembles the marten in size and color. When the snake catches a large animal, such as a squirrel or rabbit, he half swallows it and lies with it in his mouth, until it is partially digested, so it can be swallowed. As long as food is available, the snake remains in one place.

A peculiar trait is attributed to the rattler. It is said that he hypnotizes small animals and birds which are his prey. He does it in this fashion: He lies under a tree where there are squirrels and birds, and fixes his gaze on one of these animals. Although the animal may be high up in the tree, it cannot escape. It gives a peculiar cry, which is easily recognized as a distress signal. At first, the animal being hypnotized, hops higher into the tree, then down, then up again and finally further down. Each time the animal gets closer to the ground, the distance of his attempted upward retreat grows shorter. The snake lies at the foot of the tree with his eyes fixed on the animal. So intent is he upon his prey, that his attention cannot always be distracted by yelling. The animal comes closer and closer to the snake, which is lying open mouthed at the base of the tree. Finally, with an agonized cry, the victim jumps into the awaiting mouth, where it is quickly swallowed. If it is too large to be swallowed, the snake licks his prey with his tongue and closes his jaws on it several times, maiming it, so it can be swallowed.

The hypnotic spell can be broken, if the snake is forced to look elsewhere or is killed. A bird released from the spell will fly away instantly, and a squirrel will flee death the minute the eyes of the snake wander.

Although the snake does not always lie at the base of the tree, but occasionally several famnar from it, the animal is supposed to go down the side of the tree nearest to the snake, and it does not attempt to go any other direction.

This is the information which I received from North Americans, both commoners and aristocrats, learned and unlearned. I have never observed this reaction myself, and I find it difficult to believe. Among hundreds who told these tales, only 10 or 12 assured me that they had witnessed it with their own eyes. The above information was substantiated by reliable men who almost dispelled my doubts as to the veracity of these tales.

It seems to me that this supposed hypnotism might readily be explained. In North America birds are so tame, that one can come close to them when they are hopping

about the ground, feeding. A bird might inadvertently come close to a snake and be struck. The bird would have difficulty in reaching the safety of the tree without resting or collapsing, and the snake could readily overtake it. An American woman gave me information which seems to substantiate this. She saw a rabbit running fast along the road. A short distance from her, it fell over as if it were dizzy. She suddenly became aware of a rattler, following close at the heels of the rabbit. She did not tarry.

When hunted by a cat, birds fly around him at a safe distance making a characteristic cry. If nesting nearby, the bird makes loud cries and flies nearer. The cat goes calmly on his way, as if the fuss did not concern him; but gets his chance, when the bird grows bolder, and flies nearer in an attempt to peck his back. Small birds in America are quite fearless. Those nesting near the road often fly close to the face of a person passing by. Sparrows chase hawks, small birds scream at their enemies and grow bold if not approached. Might not the bird, because of curiosity, approach the snake whose eyes are bright and burn like fire when he is angry or attentive? His vile stench could cause the prey to become ill or dizzy. All these factors could contribute to a belief in his supposed hypnotic powers.

Of all the snakes, the rattler is probably the slowest traveler; therefore, it is difficult to see how he can feed on such fast animals as birds and squirrels. Perhaps the Creator has endowed him with a special ability to attract his prey. If this is hypnotism, nature has endowed other animals with similar traits.

In America, it is believed that the stare of a rattler can so hypnotize a person that he will go to the snake to be bitten. I did not find this to be true, although I stared at a rattler intently and he at me after he had been provoked. Ohers who have repeated this experiment have not found the rattler possessed of any power. I was told of a man who attempted to get close enough to watch a rattler hypnotize a bird. In doing so, he stepped on a stick which touched the snake, who turned on him with burning hatred in his eyes. For a moment the man shook life a leaf and was glad to escape from the scene. He felt he might have been hypnotized, had he not moved quickly.

Mr. Bartram, who was born in America, and Mr. Colden, who has resided there for thirty years, are both well versed in the natural sciences. They were questioned, together with others, on the behavior of the rattler when he is imprisoned, when he is free to hypnotize animals put in with him. These gentlemen all gave the same answer. The snake when imprisoned refuses to eat, and finally starves to death. He may live a half a year without food, but no matter how many animals, which are normally his food are thrown to him, he will not eat any of them. He may kill them. This I relate in answer to those who insist that they have placed small animals with a caged rattler, and seen them so hypnotized that they have jumped into his moth to be eaten. I, myself, did not have an opportunity to make this experiment.

Some say that the snake does not poison that which he is about to eat, because they think it would kill him. On this I shall not comment. I do know that dogs eat animals which have been killed by snakes with no ill effects.

Savages consider themselves masters at treating rattlesnake bites, if their remedies are used in time. However, there are two conditions when the bite is considered fatal: (1) If the rattler is angry, and strikes so deep that his fangs reach the blood vessels leading to the heart. No remedy is effective and the patient dies in a short time. If he does not die immediately, the savage, knowing the case is hopeless, uses those medicines which will make death less painful. Mr. Evans, who made the fine map of Pennsylvania, and Mr. Bartram had an interesting experience, which they related to me. They accompanied an ambassador from the government of Pennsylvania to the Iroquois, who are called the Onandago savages. When they reached the Onandagos, a savage came forth and said that he could let a rattler bite him without being harmed. In order to illustrate his skill, he took hold of a rattler and permitted it to strike his hand at close range. Remedies were immediately applied and the poison had no effect. The snake struck several times without effect, but finally the savage grasped the snake by the tail. It was greatly irritated by this action and swung around striking the man in the arm. The most effective herbs recommended were used to no avail. In spite of all his knowledge the savage died in a few minutes. He must have had confidence in the efficacy of his herbs, but they were useless when the venom was shot into his veins. It was thought that the savage, who had just returned from the land of the Senecas, used Senega rattle-snake-root or Polygala[6] which is

6 *Polygala Senega* L.

abundant there. (2) Remedies are also ineffective when a pregnant woman is struck by a rattler. The savages again elect not to use their medicines.

The rattler, which is so courageous and dangerous that it does not get out of the way of man or beast, has found its master in the pig. As soon as he is aware of the pig, he loses all his courage and flees, knowing the pig is his conqueror. Pigs relish rattlers, are capable of detecting their odor at a great distance, and run after them with bristles on end. The snake is grabbed, shaken and eaten with no ill effects. However, the head is usually left intact. Pigs eat rattlers readily, but are not much interested in other snakes. When a new farmstead is to be established where rattlers are abundant, pigs are brought in. One can rest assured that, within a short time, one will be free of these pests. Undoubtedly pigs are struck occasionally, but the venom does not harm them.

The rattlesnake is more easily killed than any other snake for he is exceedingly clumsy. A light blow on the back is usually fatal.

The body does not wriggle for half a day after the head has been severed, as is the case with European snakes. Even when the head is not severed, and no sign of injury can be detected, the snake is lifeless and motionless in less than an hour.

Because of its warning rattle, the snake betrays its location and can be destroyed quickly. It is rarely seen in the European settlements in America, although other snakes are relatively common, and may be seen every day during the summer.

When the Swedes first came to America, a superstition was prevalent among the savages, which prevented them from killing rattlesnakes. This superstition still persists in the hinterlands, where the savage who comes upon a rattler does not disturb it, but says in passing, "You go your way and I'll go mine." Because of the merciless extermination of the rattlers by the Europeans, their numbers are greatly diminished. The savages are less superstitious than formerly, and have begun to kill snakes too.

Rattlesnake meat is eaten as a remedy for certain diseases. There are people who eat the flesh and fat because they like it. If the meat is to be eaten, the snake should be killed instantly and not teased. When he is ill tempered, he bites himself and dies like one of his own victims. If the meat is eaten from a snake that has poisoned itself with its own venom, it may cause death.

Oil is made from the fat of the snake, by placing the fat on a plate in the sun. The oil is stored in glass bottles. It is thought to be incomparable in treating aches, even those due to broken bones and bruises. The oil is rubbed on the sore or aching part. It is also said to be effective in treatment of snake bite.

Instances have been reported of individuals who were bitten, but escaped discomfort, by eating the heart and liver raw and warm from the snake. There are also instances of individuals who followed this treatment, and still suffered from fever. This treatment is said to be less effective than drunkenness.

Savages use belts made from snakeskin with the rattles still attached. Europeans wear them as a protection against all types of sickness such as backache. Women wear them during childbirth to promote an easy delivery. The backbones are worn around the neck as a protection against ague and fevers. They are hung around the necks of children during teething.

The skin is used as a covering for sheaths of swords. It is said to be quite strong.

Now I shall discuss briefly the remedies which are especially recommended in the treatment of the bite of this snake.

Various plants in North America are known as snake root that is *Skaller-orms* rot or *ormrot*. They are supposed to cure various kinds of snake bite. I have no idea which of these plants is most useful. The savages in one community use one type, while those in another use a different type to treat snake bite. Usually where one of these plants occurs, the other does not.

Collinsonia[7] Linn. Spec. Plant. T. 1. p. 28.—Mr. John Bartram described the case of a savage who had been bitten by a rattler. The victim failed to respond to the usual remedies. Her swollen tongue hung out of her mouth and would not move. One of the savages made a decoction, by cooking the tops of *Collinsonia*, which was poured into her mouth. Shortly the victim indicated with her hand that she desired more, since it brought relief. More of the liquid was poured into the patient's mouth, and soon the swelling of

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[7] *Collinsonia canadensis* L.

the tongue decreased, and it returned to its normal position. Improvement was rapid and recovery soon complete.

Sanicula flosculis masculis pedunculatis hermaphroditis sessilibus.[8] Linn. Spec. Plant. T. 1. p. 235.—The snake bite wound is cut or scraped. The crushed root of this plant is then placed on the open wound. The poison is said to be drawn out in a short time.

Actaea racemo ovato, fructibusque baccatis.[9] Linn. Spec. Plant. T. 1. p. 504. *Aconitum baccis niveis.*[10] Corn. Canad. 76.— Above Albany this plant is called snake root. Many consider it the best medicine for snake bite. If this plant is held in the hand while a rattlesnake is being handled, he is not apt to bite according to one tale. Another says the snake will withdraw in fear, if a stick is pointed at him with this plant attached to it. The savages along the Mohawk always employ this plant as a remedy for snake bite. Those, who are able to handle snakes with their bare hands without injury, are usually considered to be sorcerers.

Sanguinaria.[11] Linn. Spec. Plant. T. 1. p. 505.—This plant is used as a type of remedy for snake bite by the Mohawk savages who live above Albany. The root is chewed and placed in the wound. This may well be what Mr. Dudley describes in *The Philosophical Transact.* abridged v. VII. P. 411.

Ranunculus hirsutus, foliis ternatis multifidis, calyce reflexo, fructo oblongo.[12]—This plant grows in moist places and near springs in North America. The snake bite is cut open and the crushed root is put into the open wound. Shortly, the pain is drawn out. This root is used in the treatment of the bite of a small rattler, which is thought to be more venomous than the larger ones.

Thymus foliis ovatis acuminatis serratis, corymbis lateralibus terminatricibusque pedunculatis.[13] Gron. Flor. Virg. 64.—In the English colonies it is called *Dittany.* Juice crushed from the leaves is taken with milk or other liquids. It is supposed to be an excellent remedy.

Polygala caule simplici erecto, foliis ovato-lanceolatis alternis integerrimis, racemo terminatrice erecto.[14] Gron. Flor. Virg. 80.—It is called Senega Rattlesnake root or Senega snake root. It grows in the land of the Senecas and is also found in Southern Pennsylvania. North of Pennsylvania the plant is entirely unknown. The use of this species in the treatment of rattlesnake bite has been discussed in a disputation published at Upsala under the title *Radix Senega* with Archiater and Knight von Linné as preceptor.

Serratula foliis linearibus sparsis.[15]—The root is said to be effective in the treatment of rattle snake bite.

Solidago paniculato-corymbosa, racemis reflexis, floribus confertis adscendentibus, foliis trinerviis subserrato-scabris.[16] Linn. Hort. Ups. 259.—There is a smooth leaved variety of this plant which is known as rattlesnake herb. It is so highly regarded as a remedy that both its description and illustration were published in the outstanding Philadelphia almanacs for 1737. The plant may either be ground or chewed and spit into the patient's mouth. The crushed material may also be placed directly on the wound. The patient should always swallow some of the decoction.

Artistolochia caulibus infirmis angulosis flexuosis, foliis cordato-oblongis planis, floribus recurvis folitariis.[17] Gron. Flor. Virg. 112.—An uncle of Lars Låck, who was mentioned

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[8] *Sanicula marilandica* L.
[9] *Actea rubra* L.
[10] *Actea pachypoda* Ell.
[11] *Sanguinaria canadensis* L.
[12] *Ranunculus* sp.
[13] *Cunila origanoides* (L.) Britt.
[14] *Polygala Senega* L.
[15] *Vernonia ?* sp.
[16] *Solidago canadensis* L. or allied species.
[17] *Aristolochia Serpentaria* L.

above, cured the poison resulting from snake bite by using a decoction made from this plant. Another Swede used this decoction to cure his dog at the time it was bitten. It was also used later to ease the after effects of the poison on both the man and the dog.

Fagus foliis lanceolatis acuminate serratis.[18] Linn. Hort. Ups. 287. Castanea sativa C. B. or the Castanie-tree.—The inner bark of Castanea seedlings is cooked, and together with the decoction, it is placed on the snake bite. Patients also drink the decoction, which is said to be quite effective.

These are the plants used in treatment of rattlesnake bite. I shall now list other remedies which are frequently used for this purpose:

Various types of fat, sweet oil, lard or butter are excellent for the treatment of rattle-snake bite in both man and beast. Oil should be rubbed on the wound immediately and some should be taken internally. The best source and the one nearest at hand, according to Dr. Colden, is the snake which has inflicted the wound. Kill it, open it up and use the fat as directed. The oil made from the fat of this snake is highly valued. Dr. Colden says there is evidence that it is efficacious in the treatment of rattlesnake bite in both man and beast.

Ordinary cooking salt, a less effective remedy, is moistened in the mouth and spread over the wound, immediately after one has been bitten. This remedy was first discovered in New England by a woman who was bitten on the finger by a rattler. She put her finger in salt in order to ease the pain,which presently disappeared. She had no further discomfort from the bite. In Canada, travelers, passing through the great forests, usually carry a small sack of salt in a pocket, where it will be available immediately in case of snake bite.

Theriac is considered to be one of the best remedies.

Relief has been obtained by using the following method: Immediately after a person has been bitten, a pit is dug in the soil. The bitten member is placed in the pit and covered with mould. After several hours, the poison is thought to be drawn out of the wound into the mould.

Tobacco is another favorite remedy. Gun powder is added to chewed tobacco, and the mixture is spread over the wound. Some of the tobacco juice is swallowed. This is said to be a sovereign remedy. There have been instances where a victim has been bitten several times within three days, and the tobacco cure has still been effective.

A boy who was bitten escaped poisoning, because his father sucked the poison from the wound. He was extremely careful not to swallow any saliva, and spit out all that he sucked. If this method is used, one should be certain that there are no pimples or sores in the mouth or on the gums, and that no tooth is decayed. The father of the boy did not become ill.

A man told me how he cured his son, who had been bitten by a rattler. The man took a hen and picked the down and feathers at the tail. The bare part of the hen was placed against the wound made by the rattler. The poison passed from the wound into the hen which died. Five hens died in this fashion, but the sixth and last was only slightly sick. The boy recovered completely.

This is what I learned about the remedies used in treating the bite of the rattler. In the disputation previously mentioned, *Radix Senega,* several others are given.

I shall list some of the authors who have written on this subject. Mr. Catesby's *Natural History of Carolina* vol. II p. 41 tab. 41. contains an incomparable illustration. *The Philosophical Transactions* N. 396, p. 292., N. 399. p. 309. Salmon's *Modern History* vol. III. p. 434. *The Philosophical Transactions* abridged vol. V. Part II. p. 162. *Charlevoix Hist. dela nouvelle France.* T. V. p. 233. 234. Lawson's *Natural history of Carolina* 129. fig. Disputation under Archiater and Knight von Linné *Praesid. Museum Adolpho-Fredericianum* p. 20. and the previously mentioned *Disputation Radix Senega.* —ESTHER LOUISE LARSEN, Conshocken, Penna.

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[18] *Castanea dentata* (March.) Borkh.

Record of Zoraptera in Indiana

The known range of *Zorotypus hubbardi* Caudell has been greatly extended due to the efforts of many collectors since the publication of Gurney's synopsis of this insect order in 1938 (Proc. Ent. Soc. Wash. 40(3):57-87).

Indiana is the most recent addition to the list of states where *Z. hubbardi* is known to occur. This list includes Tex., La., Miss., Ala., Ga., Fla., N. C., Va., Md., Ohio, Ky., Tenn., Ark., and Mo. On August 26, 1956, 48 specimens were taken from a sawdust pile near Chelsea in Jefferson County, Indiana, by Koestner, Riegel and MacMahon. Of these specimens the adults (18 males and 10 females) were all blind and wingless, but one nymph had developing compound eyes and long wing pads. Most had been feeding on fungus spores.

In collecting these insects in the man-made microhabitat of sawdust piles we have noticed that the age of the sawdust, amount of moisture, temperature of the pile, texture of the chips, and even the type of wood may affect their abundance, and that the presence of suitable fungi for food seems to be absolutely necessary. From the dates we have collected alate adults and mature nymphs it would seem that production of winged forms is continuous throughout the growing season.—GARLAND T. RIEGEL, Eastern Illinois State College, Charleston, and E. J. KOESTNER, Dayton Museum of Natural History, Dayton, Ohio.

Book Review

PSYCHOLOGY, EVOLUTION, AND SEX. By Cecil P. Martin. Charles C. Thomas, Springfield, Illinois. 1956 xiii + 166 pp. $4.75.

Professor Martin has written what he calls "a very unorthodox book. It does not view the problem of evolution from the standpoint usually taken by modern geneticists. . . . It exposes serious or insurmountable weaknesses in the mutation-selection theory . . . it points out an alternative theory. . . ."

The alternative is Lamarckism, supplemented by the hypothesis that Dauermodifications (here called "lingering modifications") provide the means for transmitting acquired characters. He believes that lingering modifications can be demonstrated in all groups, and he has built an inferential argument according to which they progressively deepen and are finally impressed upon the chromosomes to become truly hereditary. Sex is interpreted as being fundamentally a damper upon this system. The reviewer believes that many of his examples represent the well known fact that the gene determines a reaction norm rather than an absolute character. However, his data deserve an unprejudiced reexamination.

It is difficult for a geneticist to review this book, for the author declares that "they have an amazingly keen eye for microscopic flaws in arguments brought against the mutation-selection theory, or for alternative theories." Let it suffice, then, to mention some major defects in the book. There is no reason to doubt the author's sincerity when he says "I have tried to be fair," but his bibliography of nearly 300 titles bespeaks profound prejudice. Every reference is carefully given when it is considered in the text to support Lamarckism or to discredit the mutation-selection theory. Authors are mentioned who support the mutation-selection theory, but their papers are not cited (except when quoted for defects in their views).

Throughout the book, responses of organisms are stated in volitional terms, a practice of very doubtful validity in the majority of cases. Yet Martin must attach importance to this, for it seems to be the sole reason for the inclusion of *psychology* in the title.

Criticism of the mutation-selection theory is a healthful thing, but Professor Martin's criticisms seem to be based upon misconstructions of genetical and evolutionary theory. His major point, however, is that geneticists have been beguiled by a few established facts into acceptance of a theory for which those facts are really inadequate. He believes that a strong inferential argument supports Lamarckism. Certainly it is possible to be beguiled by a few certainties into acceptance of error; but can inference, unchecked by any fixed points, really be a better guide to the interpretation of nature? Surely, Professor Martin cannot believe this, for he has tried valiantly in this highly interesting book to give his theory the same sort of factual basis which the mutation-selection theory enjoys.—EDWARD O. DODSON, University of Notre Dame, Notre Dame, Indiana.

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